1971

Ecological Life History of Rudbeckia Occidentalis Nutt.

Juan A. Florez

ECOLOGICAL LIFE HISTORY OF RUDBECKIA OCCIDENTALIS NUTT.

by

Juan Arturo Florez

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Range Ecology

Approved:

Cyrus M. McKell
Major Professor

Committee Member

Arthur H. Holmgren
Committee Member

DeVere R. McAllister
Committee Member

William A. Laycock
Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1971

ACKNOWLEDGMENTS

The Forest Service provided the financial support for this study. My sincere appreciation is extended to Dr. Walt McDonough, under whose direction the study was conducted, for his encouragement, advice, and critical reviewing of the manuscript.

I very much appreciate the many hours of concern and logistics that have been freely given to me during my study by Dr. Cyrus McKell.

I also express my appreciation to other members of the supervisory committee for their helpful suggestions: Drs. Neil West, DeVere McAllister, Arthur Holmgren and William Laycok.

To the Agrarian University--LaMolina, Peru--who granted the author a leave of absence to conduct graduate studies, to the Rockefeller Foundation, who granted the scholarship, to the Range Science Department, his sincere appreciation and thanks. Also, the author wishes to acknowledge the devoted typing of this dissertation by Mrs. Charell Harris.

Finally, to my wife, Vicky, and my daughters, Monica and Jessica, for their patience and support in fulfilling this assignment, I extend my gratitude.

Juan Arturo Florez

Juan Arturo Florez

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

LIST OF TABLES (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

ABSTRACT

Ecological Life History of Rudbeckia occidentalis Nutt.

by

Juan Arturo Florez, Doctor of Philosophy

Thesis Director: Dr. Walt McDonough
Major Professor: Dr. Cyrus McKell
Department: Range Science

Phenological studies of coneflower on aspen range in Northern Utah showed that resumption of growth of mature plants begins at the time of snow melt and the initial or rosette stage is completed between mid-May and mid-June. The rate of growth in this stage is controlled by temperature, being greater at higher mean temperatures. The bolting stage is completed about 1 week after the initiation of stem elongation and the process of capitulum development is begun. Flowering is initiated between late July and mid-August. Cross-pollination is necessary for seed set which is completed by the end of August. Seed dissemination is begun at that time and is completed by the middle of September. Altitude appeared to have an effect on the extent of seed filling, since collections from higher altitudes had lower percentages of filled seeds.

Seedling mortality increases as the season advances and reaches a maximum at the end of June when the associated species begin rapid growth. During the first season seedling growth is restricted to one unelongated stem

and three leaves. Shoot/root ratios indicated that the main development during this season is in the roots.

Optimum controlled conditions for seed germination are alternating temperatures of 25 C-15C with 8 hour photoperiods coinciding with the periods of higher temperature. A constant temperature of 25 C or alternating temperatures of 15 C-5C or constant darkness under any of the temperature regimes give lower germination percentages.

Growth chamber studies demonstrated that coneflower is a long day plant since normal development to the seed setting stage is obtained under 18 hour photoperiods but not under 12 hour photoperiods when temperature alternations of 25 C-15 C are used. Low temperature stratification of the crown buds is not required for normal development.

A series of field experiments showed that coneflower does not inhibit the growth of an important associated grass species--mountain brome. Laboratory experiments with foliage leachate gave no evidence of inhibitory effects on the germination or growth of other species. Force-feeding of sheep with whole dried plants collected at the seed set stage showed no toxicity for these animals.

Total non-structural carbohydrates increase in the aerial parts of the plant as the growing season progressed up to the seed set stage and decreases thereafter until death of the aerial parts. Carbohydrates in the roots show a reverse trend.

Two or three clippings applied to the rosette stage resulted in death of the plants. Failure of regrowth after these clippings was probably due to exhaustion of the supply of mature buds on the crown rather than being due to exhaustion of food reserves since significant concentrations of non-structural carbohydrates were still present in the roots of these dead plants.

(181 pages)

INTRODUCTION

Ellison (1954, p. 89) said:

> Like all mountainous land of the west the Wasatch area in Utah is vitally important to people of adjacent valleys. It furnishes their drinking water, the irrigation water on which nearly all their agriculture and industry depends, and summer forage for many of their livestock, as well as timber for local use, opportunities for outdoor recreation and a habitat for wildlife.

At elevations of 1800 to 2700 meters, scattered aspen-dominated plant communities are found in northern Utah. In this important type, the forage productivities are possibly the highest per unit area of any of the western range types. The type ranks second only to the ponderosa pine type for overall productivity. This is probably due to the optimum levels of precipitation, combined with moderate temperatures during the growing season.

Characteristically, aspen stands open as the stand matures. Sufficient light then penetrates to the forest floor to permit the development of an abundance of herbs and shrubs. In these open stands where grazing has not been excessive, the forage present is generally quite desirable for grazing. It consists of a good balance of grasses, forbs and shrubs that are taken readily by both sheep and cattle. According to Costello and Turner (1944) 10 to 15 species of grasses, 20 to 40 species of forbs and several shrubs are recorded in each 100 square foot plot sample. Houston (1954, p. 2) said:

> The normal species composition of the understory, which may contain almost any proportion of grasses, forbs, and brushes, varies considerably throughout the region. Although the dominance

of a single species--aspen--suggests uniformity, some 300 understory species have been identified on aspen ranges and combinations of these 300 species are almost limitless.

In northern Utah, excellent aspen range will produce up to 1400 pounds of air dry forage per acre and will support livestock at the rate of 0.6 to 1.0 acre per A.U.M. Good range produces between 800 to 1200 pounds of forage, fair range between 800 and 350, and poor range less than 350 pounds. The Soil Conservation Service estimates that many of the aspen ranges in northern Utah are capable of up to 2600 percent improvement.

Aspen ranges are best used in the summer by livestock. Also, aspen ranges are important for deer and elk during the summer. These animals can give significant competition to livestock, especially on cut-over areas. However, the understory of most aspen ranges has been greatly altered by years of overgrazing. As the palatable species were eliminated by close and repeated use, the change has been toward dominance by lower growing, more drought-resistant, and less palatable species. One of these species which is considered to be an "increaser," is Rudbeckia occidentelis Nutt. or Western Coneflower usually found in ranges in fair to poor condition. As a basis for land management plans, the range manager should know the productive potential of the type and how a particular range is changing toward or away from it. For this purpose one of the first steps is to understand the autecology and life history of this principal species that serve as indicators of range condition. The objective of this study was to complete an ecological life history of Rudbeckia occidentalis.

This investigation was conducted from 1968 to 1971, in Logan Canyon, Cache National Forest, Utah. Specific objectives were to study the taxonomy, phenology, developmental history, ecological and physiological relationships of Rudbeckia. The research follows outlines suggested by Stevens and Rock (1952), Pelton (1953) and West (1968).

LITERATURE REVIEW

Autecological Studies

Information gained from autecological studies may be expected to add to the value of some ecological concepts, for as Salisbury (1962, p. 201) has stated: "When our knowledge of the optimum requirements of all species is complete, it may be possible to give precision to the meaning of dominance, constancy, and exclusiveness."

However, few autecological studies have been published on native or naturalized species in the State of Utah. Investigations of this nature have not been as numerous as might be expected considering the contribution such studies could make toward a complete understanding and economic management of vegetation. Among these studies are: Matthews (1965), Ecological life history of tall blueball in Utah; Wood (1966), Ecological life history of budsage in Western Utah; Buchanan (1969), The life history and ecology of bur buttercup; Gasto (1969), Comparative autecological studies of *Eurotia lanata* and *Atriplex confertifolia*.

The Genus *Rudbeckia*

Species and distribution

This native North American genus was named *Rudbeckia* by the famous Swedish botanist Linnaeus in honor of the two professors Rudbeck, father and son, who had been his predecessors at the University of Uppsala (1630-1702). The vernacular name "Coneflower" is used for a number of related species of composites having elevated disks that range in shape from hemispherical to cylindric. They are additionally characterized and distinguished from related genera by their alternate leaves and sterile ray-florets which produce no achenes. Dress (1961) reported that present-day specialists in the compositae usually assign the same species to four different genera: Rudbeckia, Echinacea, Ratibida, and Dracopis. However, with careful study it is possible to differentiate them. Gleason (1958) considered about 25 species native to North America, several of which are highly variable in habit and pubescence, yet sharply defined. Among those species, the most important that he mentioned, are: Rudbeckia hirta L. (Black-eyed Susan) a biennial or short-lived perennial found in various habitats, but chiefly in disturbed or waste land, meadows, and roadsides from Nova Scotia to Florida, West to Maine, Colorado, and Texas. Rudbeckia fulgida Ait, perennial, often stoloniferous, found in various habitats from dry rock glades to moist woods or bogs, Michigan to Pennsylvania, South to Virginia, Missouri, Florida, and Texas. Rudbeckia triloba L., a short-lived perennial found in woodland and moist soil, New York to Michigan, Louisiana, and Kansas, South to Florida, Louisiana, and Oklahoma. Rudbeckia subtomentosa Pursh, perennial from a stout woody rhizome, found in prairies and low ground, Indiana to Iowa and Kansas, South to Louisiana and Texas. Rudbeckia laciniata L., perennial from a coarse woody base, found in moist places, Quebec to Florida, West to Montana, Idaho, and Arizona. Rudbeckia heliopsidies T and G, perennial from a woody rhizome, found in pine woods, from Virginia to Georgia and Alabama. Rudbeckia grandiflora (D. Don) Gmel., a perennial found in prairies, open places, and dry woodlands, Missouri to Louisiana and Texas, Rudbeckia maxima Nutt., a perennial found in moist soil, from Missouri to Louisiana and Texas.

Kearney and Peebles (1951) found R. laciniata, from Maine to Saskatchewan and Idaho, South to Florida, Colorado and Southern Arizona. They considered this species to be a showy but rather coarse plant, of which a double form known as Goldenglow is often cultivated. The plants are reported to be poisonous to cattle, sheep, and swine. Harshberger (1911) said that Rudbeckia is a genus found in the Sierra Nevada but not in the Coast Mountains, and that in the Southern Rocky Mountain forests, Rudbeckia flava Greene, is an understory species in the aspen formation. He also emphasized that in the Ozark area (which includes nearly all of Missouri, North West Arkansas, Indian territory, Oklahoma, Northern and Central Texas), there is the rock cliff formation, and the top of the bluff is occupied mainly by R. hirta.

In the western region, Blake (1931) described another species of Rudbeckia: R. californica var. glauca which is found mainly in California and Oregon. Tidestrom (1925) and Piper (1906) described another species as Rudbeckia occidentalis Nutt., usually found in the yellow pine, aspen and spruce belts of Wyoming and Utah, westward to Washington and California.

Anatomy

No comprehensive anatomical survey of the genus Rudbeckia has ever been made, so that it is impossible to give a complete account of the subject. There are, however, numerous features that are of considerable taxonomic value.

According to Metcalfe and Chalk (1950) the epidermis of the leaf of Rudbeckia not uncommonly includes groups of silicified cells. Rosettes of silicified cells sometimes surround the bases of the hairs.

Variously distributed medullary bundles, representing branches of the peripheral ring of strands, sometimes serve as an aid in the identification of species. Chalk (1944) reported medullary bundles that were usually collateral, rarely centric with central phloem, sometimes incomplete and consisting, for instance, of phloem only in Rudbeckia species. Worsdell (1919) regarded the medullary bundles of the Compositae, like those of other families, as vestigial structures to be interpreted as relics of the scattered bundle system that is believed to have existed in ancestral forms. The medullary bundles of the Compositae vary in the extent to which they are complete at different levels in an individual plant. They are usually most complete toward the upper part of the axis, where each strand consists of xylem and functional phloem, while some end blindly in parenchymatous tissue. Within a genus, the stem of some species contain medullary bundles while they are absent from others, e. g., in Lactuca and Rudbeckia. Plants devoid of medullary bundles are regarded by Worsdell (1919) as more specialized than these in which they are present.

Phylogenetic notes

Battaglia (1951) reported that the female gametophytes of angiosperms show not only embryo sacs with haploid eggs, but also with non-haploid eggs. The different types producing non-haploid gametes may be conveniently subdivided into principal (most common) and secondary types (rare cases). Within this last type, the possibility that accessory or supernumerary micronuclei may produce the micropylar cells of a mature embryo sac is testified to by certain cases discovered in the genus *Rudbeckia* (*Rudbeckia* I type. -*R. laciniata*). Also in this genus very peculiar modes of development that lack synergids and egg cells are found (*Rudbeckia* II type. -*R. speciosa* and IV types). Finally tetraploid eggs may originate through the cytological mechanism of double restitution (birestitution nucleus). Such tetraploid birestitution nuclei were also observed in *Rudbeckia* (*Rudbeckia* IV type).

Growth and development

Very little information about *Rudbeckia* is found in the literature, especially in reference to *Rudbeckia occidentalis*.

Sampson (1917) reported that *R. occidentalis* begins to grow in rosette form as soon as the snow melts. The flower stalks are mainly produced between July 5 and August 10 and the seeds matured between August 15 and September 1. While the time of flower stalk production and period of seed maturity are influenced by physical factors, even greater contrast is brought about by weakening of the vegetation due to overgrazing.

Bleak (1961) studied the germination in the field of 67 different species, *Rudbeckia occidentalis* included, and found that seeds removed from the soil in early fall, seed removed from the soil after permanent snow, and seeds harvested fresh from the field and tested on two different dates (a few days old, and 1 year old), gave the following results in percent germination: 98.0 (early fall), 98.0 (after permanent snow), 90.3 and 94.7 (a few days and 1 year old). The same scientist made plantings of *R. occidentalis* in two areas at Ephraim Canyon, less than 2 miles apart, but with slope and exposure quite different. The first area was Philadelphia Flat at an elevation of 10,000 feet. This area is frequently covered with snow from October or November to May or early June and subject to floodings. The second area was Summit Enclosure with a west-facing slope of 8 percent and an elevation of 10,200 feet. Here the snow depth in winter is less than at Philadelphia Flat due to faster melting in the fall and spring, and also due to wind action.

The plantings were done in the fall with 100 seeds replicated three times. Seedling emergence and seedling mortality counts were made in each area just after snowmelt and several later dates. The results are shown in Table 1.

Seeds of this group did not germinate in the fall or winter while the soil was cool, but germinated after the soil warmed up in the spring, or germinated readily at 68 to 82 F in the laboratory.

Sampson (1923) reported that few plants are of greater interest to the stockmen than western coneflower because of the pecularities of its forage value

Table 1. Average field emergence of Rudbeckia occidentalis per 100 fall planted seeds and seedling mortality in two locations on three dates, after spring snow melt (1960) from Bleak (1961)

	Location					
	Philadelphia Flat			Summit Enclosure		
	Spring 6/2	Summer 7/10	Fall 9/12	Spring 5/31	Summer 7/5	Fall 9/11
Emergence	0.0	0.0	0.0	0.0	34.7	34.7
Mortality	0.0	0.0	0.0	0.0	34.0	34.3

and also because it serves as an "indicator" of range condition. He also mentioned that because western coneflower is seldom grazed "to the last leaf," its forage value is often underrated. However, the Forest Service Range Plant Handbook (1937) states that "coneflower" grows from the ponderosa pine zone up to and including the spruce zone, usually in moist but not saturated soil, but sometimes in moderately dry, poor, shallow soil. Open or shaded stream-banks, hillsides, and well-drained mountain swales, open parks and partially shaded slopes in open aspen stands are its favorite sites. It is perhaps more prevalent in Utah throughout the aspen zone. Before the normal plant cover in certain ranges of the Wasatch Mountains of Central Utah was disturbed by continued past overgrazing, with resultant erosion and soil impoverishment, coneflower was not so extensive or abundant as it is now. These conditions resulted in the decrease in density of the more palatable species, and greatly accelerated the invasion of these lands by coneflower.

Although coneflower is low in palatability or even worthless on most ranges, on some sheep or common use areas it is fair or occasionally fairly good. Furthermore, in spite of its usual low palatability, it often supplies considerable forage by virtue of its commonness, large size, and abundant, large leaves. Even when young, the stems are too tough and woody for consumption by any class of livestock. Cattle and horses do not relish the flower heads as do sheep, but those parts are often above the reach of sheep. However, seeds furnish considerable bird food.

The Forest Service Range Plant Handbook (1937) also reports that the stems of coneflower are unbranched except occasionally near the top. The leaves vary considerably in size, but average about 2 1/2 inches wide and 5 1/2 inches long on the main body of the plant. The slightly winged leafstalks (petioles) of the basal leaves are several inches long and become increasingly shorter near the top, where the leaves become stalkless (sessile). Near the apex of the stem, the leaves are fewer and much reduced in size, making the cone-like, dark brown flower heads at the apex very conspicuous. These heads start as small buttons, which gradually elongate until at blossoming time, about the middle of August, they attain full growth and may then become 2 inches long. Marked variations in size of the plant and its parts may occur, due to sit conditions.

In relation to the nutritional value of coneflower for wildlife, Knowlton (1960) studied winter food habit of moose, based upon feeding site observations, and separated seasons of use into an early winter period when the moose were still above 7,000 feet elevation, and a late winter period when the moose were in winter concentration areas below this elevation. Browse species constituted 96.9 percent of the 14,540 instances of use from 13 feeding sites in the early winter period. Forbs constituted 2.9 percent and grass and grass-like plants 0.2 percent of the instances of use. From the 2.9 percent of use of forbs, 0.1 percent were in R. occidentalis.

Flowering

Flowering in species of Rudbeckia has been studied by many scientists, especially photoperiodic responses.

Austin (1938) studied five groups of 9-19 plants of Rudbeckia bicolor, Nutt. subjected to the normal winter photoperiod of Ann Arbor, Michigan, and supplemented by artificial illumination to 20 hours. The intensity of the artificial light reaching the group nearest the light source was 56 foot candles and that reaching the farthest group was less than 0.2 foot candle. The temperature of the greenhouse was 56-65 F by day and 50-55 F by night. The Rudbeckia plants in the first three groups (nearest the source of artificial light) developed bolted stem, budded and flowered. Those in the last two groups remained in the form of leaf rosettes. For this species, the critical intensity of supplementary light (intensity necessary to supplement the normal photoperiod effectively) lies between 0.4 and 1.8 foot candles.

Photoperiodic after-effects were discovered in Cosmos bipinnatus by Garner and Allard (1927) and have since been observed in several other species of composites. Murneek (1936) found that when Rudbeckia hirta plants were transferred from long to 7 hour photoperiods, some plants failed to bloom, some plants formed the usual type of flower heads (except that these were either sessile or borne on short peduncles, the plants remaining in the rosette condition), and some bore "vegetative flowers" with green petals and more or less vegetative stamens and pistils.

The species of Rudbeckia have generally been classes as long-day plants, but Roberts and Struckmeyer (1938) found that R. laciniata, a long day plant, consistently remained a rosette and failed to produce stems in previous short day experiemnts (temperatures of 60 to 65 F), followed by long days. On the other hand, when grown at 55 F under long days, it not only produced stems, but formed blossom buds in the short day treatment at the same temperature after a relatively long time--a definite refutation of the commonly reported habits of this plant.

Greulach (1942) in Rudbeckia hirta observed photoperiodic after-effects. The plants were kept under photoperiods unfavorable for reproductive development for 28 days after planting the seed and then were subjected to from 1 to 20 or 30 induction photoperiods of a length which favored initiation of flower primordia. They were then transferred to photoperiods not favoring such development and maintained there for the duration of the experiments. Rudbeckia plants bloomed sparsely after exposure to a minimum of 17 photoperiods. Photoperiodic inhibition of stem elongation by the short photoperiods of the transfer occurred in all the plants, even in the plants which bloomed. Also, the short photoperiod inhibited vegetative growth. Reproductive-vegetative interphases, which may be considered as initial stages in rejuvenation, occurred. A number of "vegetative flowers" with green petals and more or less vegetative stamens and pistils developed on plants of Rudbeckia hirta.

Alternating periods of light and darkness were studied by Garner and Allard (1927) in Rudbeckia bicolor L. With a total daily illumination of 12 hours, progressive shortening of the alternations of light and darkness resulted in decided decreases in growth. A minimum was reached with light-darkness alternations of about 1 minute, while further shortening of the alternations to 15 seconds gave decided improvement in growth. The 1 minute periods induced chlorosis. Altman and Dittmer (1962) reported that Rudbeckia bicolor produces a photoperiodic response, occurring at relatively high temperatures and a photoperiod longer than 10 hours. Also the reproductive development is promoted by high temperatures during photoperiodic induction.

The effect of gibberellins in the growth and development of Rudbeckia, was studied by Chailakhyan (1957). Gibberellin was applied in concentrations of 0.02 percent as drops in the center of Rudbeckia rosettes, resulting in the formation of stems, flowers, and fruits under short day conditions. He suggested that gibberellins may lead to the formation of substances essential for flowering of long-day species and that a different substance is necessary for short day plants.

Insects, pathogens and toxic substances

Aphids have been observed to be very numerous upon Rudbeckia occidentalis in various shaded canyon areas of Utah and Southern Idaho. Knowlton (1954) reported that the material examined proved to be Macrosiphum cockerelli Hottes. In September, 1945, this species was abundant on leaves and stems of these plants near the summit of Ephraim Canyon, Utah. Here a careful examination showed some syrphid larvae, adult and larval ladybird beetles, including adult Hippodamia guinguesignata Kirby and H. lecontei Muls, damsel bugs, which were largely Nabis alternatus Parshley, and Anthocoris sp. preying on this aphid. Macrosiphum rudbeckiarum (Cockerell) was collected at Mt. Nebo, Utah, and is less numerous than M. cockerelli on Rudbeckia. The same author (1942) collected and identified Mizus haywardii from Rudbeckia plants.

In relation to pathogens, during the last part of August and through September, the leaves of R. occidentalis, show a heavy attack of powdery mildew which, according to the Agriculture Handbook (U. S. D. A., 1960), was identified as Erysiphe cichoraccearum DC., and is generally found in Utah. Leaf spot in Rudbeckia is also reported to be caused by Ramularia rudbeckia P. K. found in Colorado, Idaho, Montana, and Utah.

According to Pammel (1911) two species of Rudbeckia are reported to be poisonous to livestock, viz., R. laciniata, said to be poisonous to sheep, and R. occidentalis, thought to have poisoned cattle in Kansas and Iowa. Chestnut and Wilcox (1901) record an instance where 100 sheep were turned into a two-acre timber plot and fed mainly on R. laciniata. On the second day, 20 sheep showed symptoms of poisoning and 7 died. They state also that specimens of the plant have been sent from Missouri, with the complaint that it is not infrequently fatal to hogs. Gates (1930, p. 67) reports _R. laciniata_ poisoning in swine. He cites a case:

> . . . a number of hogs, which had access to nothing else, died in convulsions with general symptoms of belladonna poisoning. . . . Fencing the animals from access to _Rudbeckia_ prevented further trouble. However, the further feeding of _Rudbeckia_ resulted in the death of the hog to which it was fed.

Hansen (1930, p. 25) writed the following regarding black-eyed susan (_Rudbeckia hirta_):

> Although experimental work on the subject is lacking, there is abundant field evidence pointing to this common wild and ornamental species as the cause of poisoning in cattle and hogs and a number of cases of this character have been observed in Indiana. In cattle the trouble is characterized by severe digestive disturbances, colic, groaning, and passing of parts of the lining membrane of the feces. In hogs, loss of consciousness, followed by awakening and walking aimlessly for hours, has been observed as a result of grazing on the roots and tops of black-eyed susan.

Skidmore and Peterson (1932) fed young plants to swine and did not produce toxic symptoms. More mature plants fed to swine, sheep, rabbit and calves produced toxic symptoms in some animals within 24 hours. Continued feeding to swine proved non-fatal. _R. lacinitata_ has a very disagreeable taste and is not readily eaten by animals unless they are very hungry.

Coumarin has been found in _R. speciosa_ and _R. laciniata_ by Lingelsheim (1928).

With reference to inhibitory effects, Carnahan and Hull (1962) reported tests that were made with leachates of _R. occidentalis_ and _Madia glomerata_ Hook. (tarweed). Chopped plant material was soaked in water at 1:10 ratio for 24 hours. Leachates of both species significantly (1 percent level) reduced the normal germination of seeds of Agropyron intermedium (intermediate wheatgrass) and Raphanus (radish). Intermediate wheatgrass leachate had no effect upon its own seeds but significantly reduced normal germination of radish.

DESCRIPTION OF STUDY AREA

Location

The study area was selected in the Wasatch Mountains (Bear River Range) of Northern Utah, within the Logan Ranger District on the Cache National Forest, Township 13 N and Range 42 E.

Geology

The geology of the study area has been investigated by Young (1939), Williams, J.S. (1948, 1956), Williams, E. J. (1964), Holland (1952), Sadlick (1955) and Taylor (1963). The main points of these studies are discussed below.

During and before the Paleozoic era, the Rocky Mountain region was under water and was called the Cordilleran Seaway. This body of water separated a string of volcanic islands along the west coast from the main land-mass of North America. Thick deposition of erosional material from mountains in the east and islands in the west occurred in the Northern Utah area. These materials solidified into rocks, primarily limestone, interspersed with shale, dolomite, sandstone or quartzite.

The sea persisted in the Mesozoic era. During late Mesozoic and early Cenozoic eras tremendous earthquakes shook Western North America. As a result, the Paleozoic rocks of the Logan Canyon area were deformed, faulted and elevated. As a consequence, the Bear River Range began to form. Another cycle of widespread accelerated erosion set in. This time a conglomerate, the Wasatch formation, covered extensive areas to the east of the Bear River Range. This was followed by more disturbances, uplift of the Wasatch formation and erosion. The presently exposed Wasatch formation consists of two members, conglomerate overlying limestone. The limestone is stromatolitic, being light-brown to cream colored. The pebble and cobble conglomerate is cemented with a matrix of sand and iron oxide. The high content of ferric iron accounts for the red color of the deposit.

In the Pleistocene epoch there was widespread elevation of the area and heavy glaciation. Tony Grove Canyon has been scoured by several glaciers. Ice of one glacier came within half a mile of the confluence of Tony Grove Creek with Logan River.

The uplifting process has by no means ceased. The valley bottoms and mountain peaks adjacent to Logan Canyon continue to rise.

Topography and Soils

The experimental area comprises about 400 acres within which three enclosures were established--two on a south-facing slope (one on the upper and one in the lower part) and one on a north-facing slope (upper location).

The percentage slope at various positions on five lines each separated by 20 m each gave the averages as shown in Table 2. The steepest position at 35 percent is on a southerly aspect with overhead tree cover. The gentlest slope of 18 percent occurs in the upper part of the unshaded slope.

Table 2. Slope percentage of various research subplots

No. of line	Aspect	
	North shaded	South unshaded
1	20	35
2	25	45
3	30	30
4	35	25
5	20	18
	130	153
Average	26.0	30.6

The texture of upper horizons of soils on aspen shaded sites is uniformly silt loam. Soil profile studies show two basic types of parent material--Wasatch conglomerate and glacial till.

At this site the surface soil was very loose and friable, and much burrowing and mixing by gophers and other small mammals was evident. This soil is closely associated with the Crab series geographically and, perhaps, genetically (Southard, 1958).

Classification

The soil of the Tony Grove Canyon area is thought to be a Brown Forest soil on the basis of color, lack of A_2 horizon and absence of profile development below 0.45 meters. The carbon: nitrogen ratio is not as wide as is ordinarily expected in a forest soil. The profile is acidic throughout as are some Brown Forest soils in the Lake States.

Soils profile

Tony Grove, loam:

Horizon	Depth	
A_o	3.5-0 cm	Mixture of undecomposed leaves and twigs.
A_{11}	0-25 cm	Very dark grayish brown, loam; fine granular noncalcareous; pH 5.5, gradual irregular boundary.
A_{12}	25-45 cm	Very dark grayish brown, loam, medium subangular blocky, non-calcareous, pH 5.3; abrupt irregular boundary.
B_1	45-100 cm	Very pale brown, clay loam, medium subangular clocky, noncalcareous, pH 5.4; diffuse boundary, few roots.
C_1	100-160 cm	Very pale brown, gravelly loamy sand, single grained, noncalcareous, pH 5.6, diffuse boundary.
C_2	160-200 cm	Very pale brown, yellowish and brown gravelly loamy sand, noncalcareous, pH 5.6.

Gravel and cobble of assorted sizes from 0.2 to 20.3 cm in diameter were encountered below 45 cm. This coarse material makes up to 50 to 80 percent of the soil volume below 45 cm.

Soil reaction and calcium carbonate equivalent

Of the areas sampled, all surface samples were acid, ranging from 5.6 to 5.3 in pH. However, changes in the pH with depth were not consistent.

The Tony Grove soil samples decreased in pH from 5.5 in the surface to 5.3 at 45 cm and then increased to 5.4 at 100 cm and 5.6 at 200 cm. The reason for this apparently is the result of the high clay layer in the A_{12} horizon. The pH values appear to be related primarily to parent material differences with the texture of the parent material modifying the extent of change in pH from the parent material. Recycling of considerable quantities of bases by the aspen (Daubenmire, 1953) tends to maintain the surface horizons at a slightly higher pH than the next horizon (25 to 45 cm).

The Tony Grove soils have extremely rocky and sandy subsoil to 200 cm or more. There is no evidence of calcareous parent material to the depths sampled. The precipitation in the area at the Tony Grove Ranger Station snow course, elevation 1,875 meters, is estimated to be 60 to 63 cm. This amount of precipitation could easily leach these soils to 160 cm, even if they were derived from calcareous parent material.

Oxidizable materials

From field colors the oxidizable material was expected to be high and organic matter ranged from 7.6 percent to 4.4 percent in the upper horizons (Table 3). All profiles had 1.5 percent or more oxidizable carbon to at least 45 cm depth. With an increase in the clay percentage in the 45 to 300 cm depth, there was a marked decrease in organic carbon below 40 cm (approximately 1/3 as much as the horizon immediately above it). This lower boundary of the horizon with the high organic matter accumulations appears to coincide with the boundary between the more rocky subsoil and the less rocky mantle above it. Nevertheless, the plant roots can apparently penetrate the rocky subsoil quite easily, but the coarse texture of the subsoil acts to discourage lateral root growth because of droughtiness and low fertility.

Such values indicate relatively slow rates of organic matter decomposition. In these areas this slow rate of decomposition is the result of long periods of snow-covered, cool climate and the prevalance of a dry season when the temperature is favorable for rapid decomposition. The accumulation is not unexpected, but neither is it abnormally high.

Particle size distribution

Although all soils are classified as loams (based on the surface soil texture), there is considerable variation in textures of the different horizons. The change in clay content with depth shows an increase from 45 to 160 cm depth, from 27.5 percent in the surface to 37 percent at 200 cm and then a decrease to 21 percent at greater depth. The reason for the accumulation of

Table 3. Chemical characteristics of samples from Tony Grove area

Soil type and depth cm	Percent organic matter	Calcium ppm	Phosphorus ppm	Magnesium ppm
Exclosure 1 (south, lower)				
0-12 cm	4.4	20.44	0.58	1.69
12-24	2.5	16.00	0.47	1.78
Exclosure 2 (south, upper)				
0-12 cm	7.6	27.56	0.49	2.22
12-24	5.5	20.44	0.33	1.82
Exclosure 3 (north)				
0-12	6.8	24.00	0.56	1.56
12-24	5.0	-----	----	----
Soil profile--south slope				
A 0-25	7.2	17.78	1.27	1.91
A 25-45	2.5	9.78	None	1.47
B 45-160	3.2	12.44	0.06	1.96
C 160-200	1.5	5.78	None	1.29

clay in the middle horizons appears to be a combination of weathering in place and colloid movement in this horizon (see Table 4). This easily explained change in clay content does not apply so easily to the silt and sand in some instances. As the clay percentage increases, the percentage of sand also increases and silt decreases. In other examples the sand increases as clay decreases.

Table 4. Particle size analysis of Tony Grove profile (averages)

Horizon		Percent sand	Percent silt	Percent clay
A_1	0-25	19	53.5	27.5
A_{12}	25-45	21	50	29
B_1	45-160	21	42	37
C_2	160-200	43	35.5	21.5

Soil moisture measurements

These measurements were made at depths of 30, 60 and 90 cm using the gravimetric method, during the growing season and for 2 years (1968 and 1969) (see Tables 5 and 6).

It should be kept in mind that as far as the plant is concerned, available moisture is the important factor. The difference in moisture retention at 1/3 and 15 atmospheres approximates available moisture.

Because of the occasional rains during the growing season, the moisture availability was not a problem for the growing plants, as is shown in Table 7.

Table 5. Mean soil moisture percentages by weight for plots at three soil depths during the period of June 14 through October 18, 1968

Date	Depth cm	Plot No. 1	2	3	Precipitation	
6/14	30	36.6	34.4	32.4	6/14-6/28	snow
	60	35.2	33.0	35.2		
	90	36.3	33.4	30.5		
7/4	30	26.9	24.2	22.4		
	60	23.4	20.3	22.4		
	90	31.1	24.8	28.3		
7/12	30	30.6	27.4	24.6		
	60	25.9	23.8	23.7	6/28-7/12	2.42 cm
	90	24.3	26.2	26.0		
7/26	30	15.1	17.1	14.7	7/13-7/26	trace
	60	16.4	15.9	11.9		
	90	15.0	18.9	20.2		
8/12	30	22.3	20.1	11.6	7/27-8/12	3.62 cm
	60	22.5	18.0	18.7		
	90	18.1	19.5	18.6		
8/23	30	32.4	29.2	25.1	8/13-8/23	8.77 cm
	60	28.1	27.3	29.3		
	90	26.3	29.3	22.3		
9/6	30	23.5	25.1	24.0	8/24-9/6	0.62 cm
	60	27.5	22.1	30.4		
	90	25.2	24.0	25.4		
9/20	30	20.7	21.2	21.2	9/7-9/20	trace
	60	26.2	21.5	29.3		
	90	25.6	25.4	24.5		
10/4	30	32.6	30.3	30.3	9/20-10/4	2.35 cm
	60	33.0	29.4	31.9		
	90	28.2	28.2	29.5		

Table 6. Mean soil moisture percentages by weight for Plot No. 1 at two soil depths during the period of June 13 through September 19, 1969

Date	Depth cm	
6/13	30	37.0
	60	35.0
6/27	30	32.0
	60	33.0
7/11	30	26.0
	60	30.0
7/25	30	22.0
	60	21.0
6/8	30	11.0
	60	15.0
8/22	30	14.0
	60	13.0
9/5	30	15.0
	60	17.0
0/19	30	13.0
	60	16.0

Table 7. Percentage moisture at field capacity and wilting point determined in greenhouse with soil of the Tony Grove area and *Rudbeckia occidentalis* as indicator (March, 1970)

No. of can	Field capacity	Wilting point
1	35.52	12.44
2	24.61	7.80
3	26.10	9.30

Climate

According to the United States Weather Bureau precipitation map (U.S. Geological Survey, 1965) the experimental area lies in the 62 cm annual precipitation zone. Most of the precipitation received is in the form of snow. Summers are usually dry with generally less than 15 cm of rainfall from May through September. Sporadic showers are expected every month during summer and widespread ones occur towards the end of July or, more often, during August (U.S. Department of Commerce, 1940 to 1968) (Appendixes I and II).

The mean annual temperature for the area is 37 F, with a July mean of 62 F and a January mean of 20 F. The average frost-free period in the aspen zone is 85 days. The average represents a period from the last 32 F temperature in the spring to the first 32 F temperature in the fall and is usually from June to September (Table 8).

Vegetation

The area of study lies within the subalpine forest zone. The climatic climax vegetation of the area is dominated by Douglas fir (*Pseudosuga menziesii*). However, relatively little of the area is covered by this since topography, soils and disturbance have greatly influenced the present vegetation. Aspen (*Populus tremuloides*) makes an almost pure canopy cover on the study area (south-facing slopes).

The unshaded exclosure on the north-facing slope is covered with abundant snowberry (*Symphoricarpos vaccinioides*) and sagebrush (*Artemisia*

Table 8. Completion of thermograph readings of air temperature in the area of study (in degrees F), 1968-1970 averages

Month	Temperatures recorded for period	
	Highest	Lowest
January	48	4
February	59	6
March	57	0
April	80	7
May	85	15
June	80	27
July	88	34
August	85	32
September	72	27
October	65	20
November	70	21
December	52	15

Annual mean = 37 F

tridentata), in mixture with bitterbrush (Purshia tridentata). Chokecherry (Prunus virginiana) and wild rose (Rosa woodsii) are shrubs of less frequent occurrence. Mountain brome (Bromus marginatus) is the most plentiful of the grasses. Goldenrod (Solidago lepida) and goldeneye (Viguiera multiflora) are common in unshaded situations. Also tall larkspur (Delphinium occidentale) and butterweed (Senecio integerrimus) are found growing in association with rather poorly developed snowberry.

An analysis of non-arboreal vegetation on the southern slope was carried out to determine their floristic composition, cover value and density. Cover as used in this study is "the proportion of ground occupied by perpendicular projection onto it of the aerial parts of individuals of the species under consideration." (Greig-Smith, 1964, p. 5) In the same way "density is the number of individuals of the same species per unit of area."

The area was sampled with 10 transects from the lower to the upper part of the south-facing slope (20 m between two contiguous transects). In each transect, 10 quadrats of 1 square meter each were selected at random for analysis. Sums of cover values of the different species were expressed in average percentages of absolute cover (Table 9).

Tree density values were estimated in the area by counting the number of trees in an area of 1,600 square meters and these values were converted to the number of aspen trees per hectare, a value of 2,874 aspen trees.

Table 9. Average density and average percentage cover of the analysis of vegetation from the Tony Grove area

Species	Average D/m^2	Average percent cover
Populus tremuloides	0.28	
Prunus virginiana	0.94	1.19
Sambucus racemosa		
Symphoricarpos oreophilus	2.11	2.83
Rudbeckia occidentalis	8.41	10.03
Senecio serra	2.39	2.04
Agastache urticifolia	10.02	3.99
Hackelia floribunda	1.65	1.16
Vicia americana	0.26	0.15
Potentilla glandulosa	0.04	0.05
Delphinium occidentale	0.49	0.34
Achillea millefolium	1.81	0.85
Aster foliaceous	0.20	0.15
Lathyrus leucanthus	0.12	0.60
Melica bulbosa		
Bromus polyanthus	15.00	8.36
Agropyron trachycaulum	4.73	6.27
Poa reflexa	0.30	0.02
Elymus glaucus	0.73	0.14
Carex occidentalis		
Collomia linearis		
Chenopodium album		
Polygonum douglasii	1.00	0.22
Phacelia utahensis	5.93	2.41
Stellaria jamesiana	0.30	0.01
Thalictrum fendleri	0.53	0.28
Balsamorhiza sagittata	0.17	0.16
Descurainia richardsonii	0.51	0.10
Madia glomerata	0.10	0.02
Smilacina racemosa	0.15	0.13
Galium bifolium	0.07	0.03
Total spp. comp. cover	58.04	41.53
Total ground cover		58.47
Total		100.00

Past use

The entire area has been regularly grazed or browsed in the past by domestic livestock during the summer months. Deer and elk also have the opportunity to use the site.

MATERIALS AND METHODS

The main objective of this study was to complete an ecological life history of R. occidentalis. The study was divided into 11 parts to accomplish this objective. Field work was completed largely within exclosures in the Tony Grove area of Logan Canyon on the Cache National Forest, Utah. Laboratory, glasshouse and growth chamber studies were done at the Forest Science Laboratory of the Intermountain Forest Research Experimental Station, Logan, Utah.

Taxonomy and Morphology of R. occidentalis

By using the published flora of the Western United States, and the herbaria of Utah State University (Logan) and University of Utah (Salt Lake City), the geographical distribution of the species was determined. By observing mature plants and seedlings brought from the field to the laboratory, a description of the morphology of R. occidentalis was made.

Phenology

Mature plants

Growth and phenological development were determined throughout the years 1968-1970. During the early part of the growing season when growth and development were most rapid, determinations were made once a week. Later in the season the determinations were made every two weeks.

The phenological development of 15 permanently marked, mature plants was studied in each of the two exclosures. The exclosures were numbered 1 and 2 and were located on a south-facing slope in the study area. Of the 15 plants in each exclosure, 10 were used for studies of aerial parts and 5 for root studies.

Measurements of the growth of stems were made each week by measuring the height of the tallest stem in each plant. Also, the number of stems per plant, number of leaves per stem and size of leaves were determined. Leaf size was calculated from measurements of the length and maximum width of the middle leaves on the stems. At the same time, weekly observations are made on the dates that rosetting, bolting, flowering, fruiting and seed dissemination occurred.

At the flowering stage, pollination was studied by observing the activity of insects visiting the heads of flowers. Also, 12 plants in 1969 and 24 in 1970 were covered with cheese cloth bags before pollination occurred. Complete counts of fruits and seeds from bagged heads were made after complete seed set in unbagged control plants had occurred.

On plants without bags, 24 heads were counted for number of seeds per head. The seeds were brought to the laboratory for germination studies. Also, measurements of the "cone" were made from 200 plants under shade and open conditions, to determine differences in size and seed production. The extent of dissemination of seeds in the field was studied by marking four plants during 1969 and six during 1970. Each mature plant was isolated from other Rudbeckia plants by clipping a 4 m radius around the marked plant. The height of the tallest

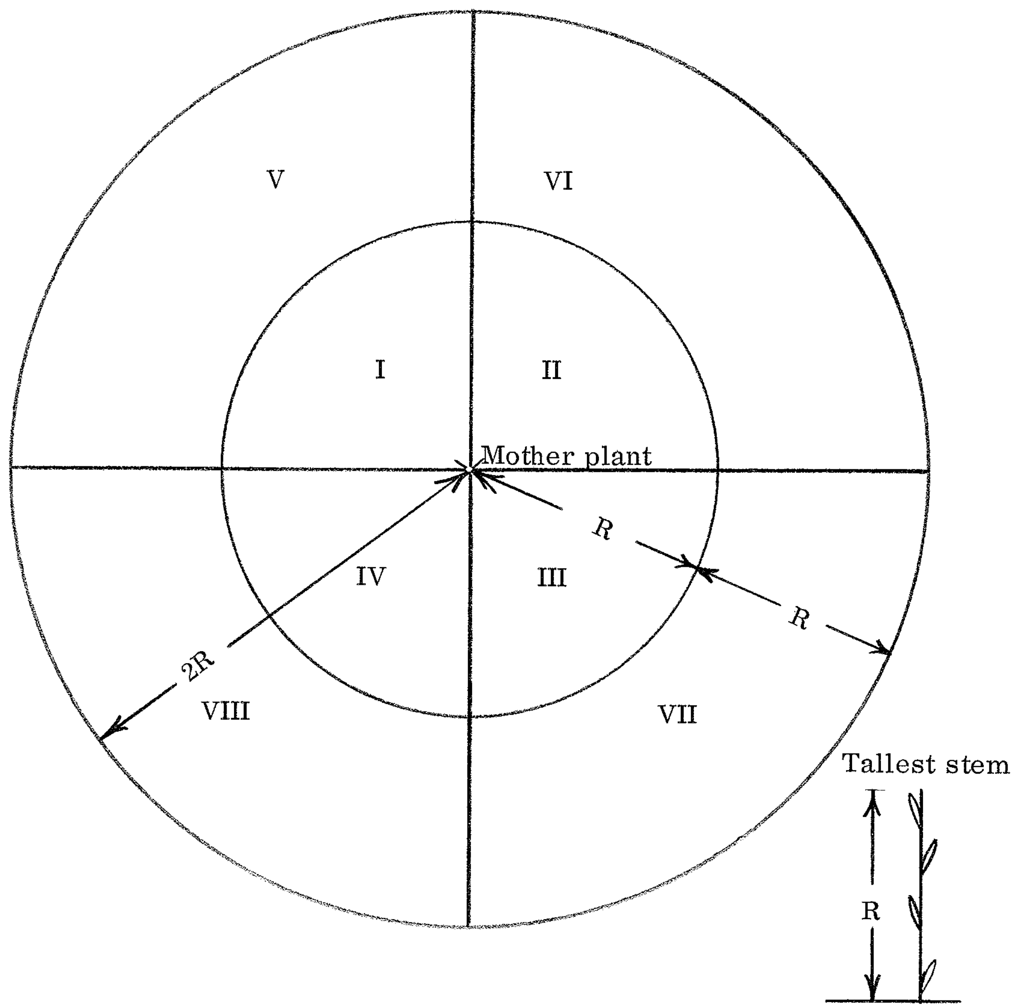


Figure 1. Distribution of the plots around each plant of Rudbeckia occidentalis for seed dissemination studies.

stem was measured for each plant. Average height of all the studied plants was taken as the length of a radius = R from each isolated plant. Two concentric circles were marked around the plant, the first with a value of R and the second with a value of 2 R. Each circle was then divided into four equal parts and enumerated in the same order, with a total of eight plots per plant (Figure 1). After "seed" fall had occurred, a layer of soil 3 cm deep from the surface of each plot was collected and brought to the laboratory; where, by placing each soil sample in a container with water, the heavy materials like soil and gravel were sedimented while the seeds floated to the surface of the water. The number of Rudbeckia "seeds" in each plot was thus counted. All seeds counted appeared to be fresh and newly disseminated; seeds from previous years would be germinated or if not viable, would be decomposed.

Seedling

Observations on seedling establishment, morphology, and survival were made along two transects of 50 m each located in exclosure No. 1 and 2. A complete analysis of the associated species along the transect were made. Also, records of the date of emergence of seedlings and of first stems from perennial crowns were determined. One hundred seedlings were marked in each transect and weekly measurement and counts were made for rate of growth determinations, number of stems, number of leaves, size of leaves, and other morphological characteristics as the season progressed. From another set of seedlings, two seedlings were taken every 2 weeks to determine the seasonal change in shoot/root ratios.

At the end of the growing season of 1969 the survival of the seedlings was determined and in the growing season of 1970 the survived seedlings were observed for a second year. Also, 100 new seedlings were observed, using the same procedures as described above.

During the winter monthly trips to the study area were made to collect plants and to observe any growth under the snow.

Seeds

Most of the seed (achenes) studies were done in the laboratory. During March of 1969 the influence of temperature and light on the germination of Rudbeckia seed was observed in two growth chambers. Two alternating temperature treatments were studied in an 8 and 16 hour cycle.

1. 25 C (8 hours) and 15 C (16 hours)
2. 15 C (8 hours) and 5 C (16 hours)
3. Laboratory conditions (constant 23 C $\pm$ 2 C)

Two light treatments were used in the same 8 and 16 hour cycles at each of the two temperature alterations.

1. With 8 hour photoperiods at the higher temperature.
2. In total darkness.

The seeds harvested during the growing season of 1969 were separated into large and small size classes to study whether size had any influence on the germination process.

Considering the results of these preliminary germination data, seeds harvested in 1969 and 1970 from 10 different sites within the State of Utah were analyzed for germination under growth chamber conditions at alternate temperatures of 25 C, 15 C and 8 hour photoperiods.

To see if the failure of seeds to germinate under certain light and temperature conditions was due to lack of viability, seeds collected from different sites within Utah were treated with 2, 3, 5 Triphenyl-2H-tetrazolium chloride.

Effect of Small Mammals

The gopher populations of exclosures 1 and 2 were estimated by counting the current years mounds within each exclosure and comparing with the gopher population index established by Richens (1964). Counts were made in July, 1969, and July, 1970, and converted to number of gophers per hectare.

Greenhouse Studies on Growth and Powdery Mildew Attack

At the time of seed set during August and September *Rudbeckia* is heavily attacked by powdery mildew in the field. Greenhouse studies were, therefore, undertaken to test the theory that mildew attacks *Rudbeckia* leaves after growth has ceased but not while the leaves are growing.

Sixteen mature plants collected in July and August of 1970 from the Tony Grove area were brought to the greenhouse and divided into four groups of four plants each.

Each group received spray treatment of gibberellic acid (GA_3) solution to promote regrowth after clipping all the plants 100 percent. The treatments were as follows:

1. 100 ppm GA_3 in one application
2. 200 ppm GA_3 in two 100 ppm applications (the second after 1 week of the first)
3. 300 ppm GA_3 in three 100 ppm applications (1 week interval between successive applications)
4. Check plants.

In all the treatments Tween 20 was used as a leaf adherent for the GA_3. Leaves were sprayed with a sufficient volume of solution (25 cc for each plant) to wet the entire surface. Observations of leaf blade and petiole growth were made and, in a scale of 0 to 10 for mildew attack, periodic quantifications were assessed according to the following scale:

0 = no attack

10 = 100 percent of plant leaf areas affected.

Samples of the leaves were brought to the laboratory from the field for identification of the pathogen than produced the mildew.

To determine whether plants that went without bolting and flowering throughout the growing season in the field yet showed vigorous growth were the result of some kind of fertilization (for example by livestock manure), fertilization studies were undertaken in the greenhouse. Two sets of mature plants (3 each) were used. One set had an application at the rate of 40 kgs of nitrogen/hectare in the form of ammonium sulfate (21 percent) and the other received none. Measurements of growth under greenhouse conditions were made.

Dormancy and Photoperiodic Studies

Twenty-eight mature plants from the Tony Grove area were collected in the late fall of 1969 and 20 of them were kept in the cold room of the laboratory during the months of October, November and December, 1969, and January, 1970. The remaining eight plants were kept for the same time under greenhouse conditions (no cold treatment).

On January 27, 1970, two Sherer-Gillett growth chambers were set as follows:

Chamber 1: Temperature alternations: 25-15 C

Light for 12 hours from 16-96 inch cool white fluorescent lamps plus eight 40-watt tungsten lamps (25 C)

Dark for 12 hours (15 C)

Chamber 2: Temperature alternations: 25-15 C

Light--18 hours: 12 hours from fluorescent lamps (25 C)

6 hours from tungsten lamps (15 C)

Dark--6 hours

In each chamber three mature plants without a cold treatment and eight plants with a cold treatment were set and measurements of height, number of stems, size of leaves, date of bolting, flowering and seed production were recorded.

During the winter 1969-1970 monthly trips to the study area were made and two mature plants were dug up, potted and brought to the greenhouse each time.

In the greenhouse two benches were prepared for different light treatments. Bench No. 1--natural greenhouse conditions with short winter photoperiods. Bench No. 2--same conditions, except that supplementary fluorescent light for a photoperiod of 16 hours was added. One plant from each collection date that had varying natural cold treatment in the field from December to March was placed on each bench, in addition to the two plants without cold treatment that had been collected from the field before the first permanent snow cover. Data recorded included growth rate, number of stems per plant, size of leaves, date of bolting, flowering, seed-set, and viability of seeds.

Composition and Flowering in Young Plants

It is possible to see that a few isolated seedlings produce heads and seeds under field conditions. However, the majority of seedlings do not do that and remain in the rosette stage. In order to determine the influence of spacing among plants upon flowering an area of 32 m^2 was prepared behind the Forest Service Laboratory in Logan and a layer of soil 20 cm thick was brought from the Tony Grove area to prepare an experimental garden for composition studies. Three treatments in plant spacing were used:

1. 20 cm x 20 cm
2. 10 cm x 10 cm
3. 5 cm x 5 cm

Seeds of Rudbeckia with 90 percent tested germination were used in each treatment. Also, another set was similarly treated by transplanting seedlings 2 weeks old that had been germinated in petri dishes in the laboratory and started in the greenhouse. The distribution of the treatments in the field are shown in Figure 2.

Using the four plants located in the center of each treatment (in order to avoid side effects), records of rate of growth, bolting, flowering and seed production dates were kept. Also, viability of seed produced was determined. Temperature data were recorded by a thermograph in the garden area.

Inhibitor Studies

In view of Carnahan and Hull's (1962) report of inhibitory effects of *Rudbeckia occidentalis* over intermediate wheatgrass (*Agropyron intermedium*) and radish, studies were undertaken to determine the inhibition of other plants by *Rudbeckia*.

Five grams of coneflower air dry leaves (picked at the seed set stage) plus 100 ml of distilled water were blended and held for 24 hours. The suspension was then filtered through cheesecloth and, also, through Whatman No. 1 filter paper. From this filtered extract, different dilutions were used to determine the effect of leachate on germination of "Manchar smooth brome" and "Nordan crested wheatgrass."

1. 1 ml extract + 3 ml water
2. 2 ml extract + 2 ml water
3. 3 ml extract + 1 ml water
4. 4 ml extract
5. 4 ml of water

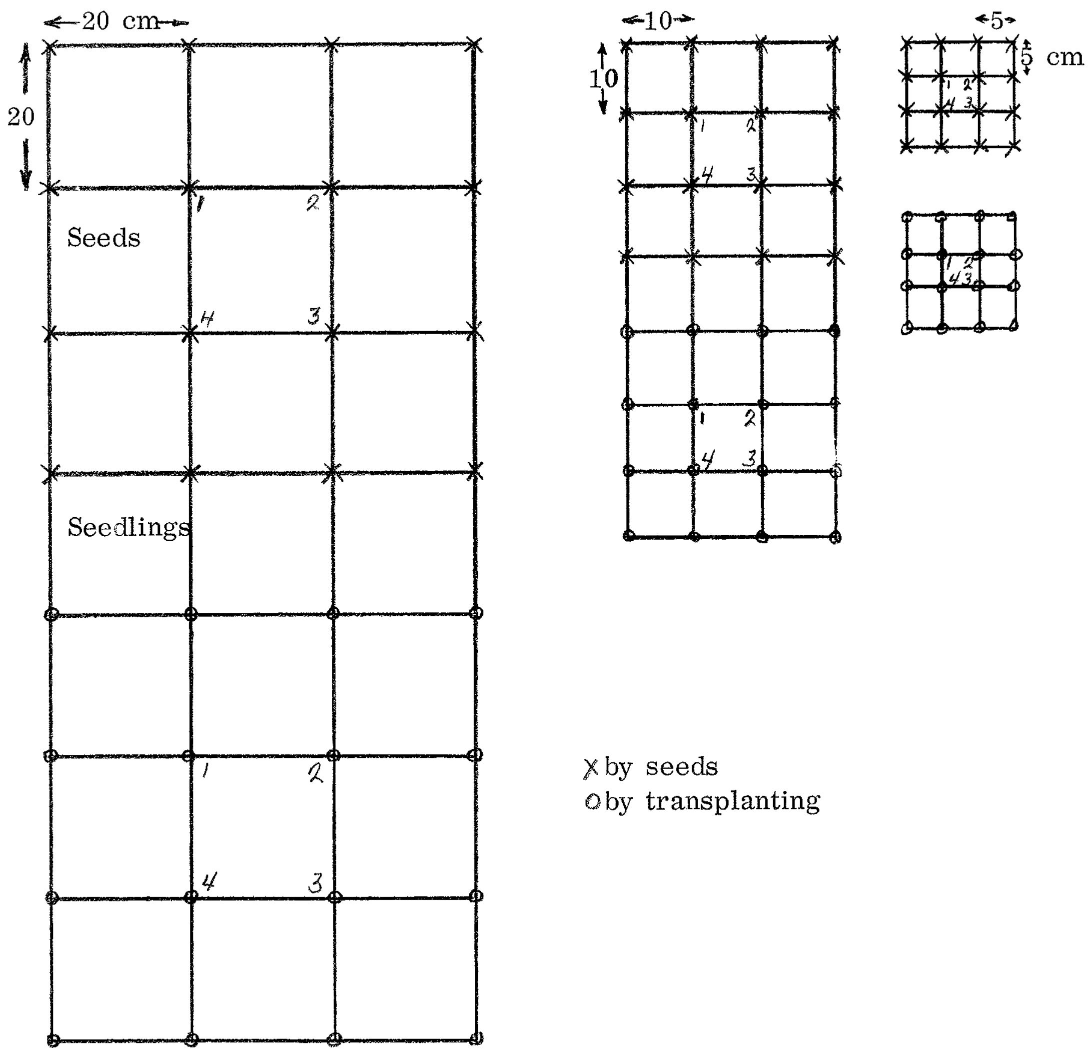


Figure 2. Distribution of seeds and seedlings of Rudbeckia occidentalis for competition studies.

After this preliminary study various treatments were used to determine the nature of the inhibitor. Then additional germination tests were run as above.

The treatments to the extract were:

1. 15 ml of extract, boil and simmer,
2. 15 ml of extract plus 1 gm of activated charcoal (Norit A) for 24 hours. Filter and centrifugated 5 minutes,
3. 15 ml of extract, dialyzed in distilled water for 24 hours,
4. extract, keep water refrigerated.

Chromatography studies were also tried using the Rudbeckia extract with ethanol, 40 percent methanol and water as a developing solvent. After 24 hours, each chromatographic paper was divided into 10 RF sections and in each section, using Agropyron cristatum (L.) Gaertn. seeds. A germination test was done. A little distilled water was added to the sections to facilitate germination.

To see if the results were conclusive for Rudbeckia similar trials were run with extract of tomato leaves and mountain brome (Bromus carinatus) in the same way.

Twenty plants of mountain brome growing within Rudbeckia stem clusters in the field were studied to determine whether "mountain bromegrass" (an associated species of Rudbeckia in the field) is inhibited in growth by Rudbeckia. Measurements of the number of stems per plant, height and length of the roots were made. Also, dry weight of root and aerial parts were recorded. The same procedure was used for 20 plants of brome similarly associated with Senecio serra (a co-dominant with Rudbeckia) and 20 plants of bromegrass growing alone.

In all three treatments comparisons in terms of shoot/root ratio, number of stems and root length were made in order to see the influence of Rudbeckia or Senecio over the growth of mountain brome under field conditions.

Clipping and Carbohydrate Studies

Clipping (harvesting) of forage was accomplished in five stages of the life cycle of Rudbeckia. The objective of this study was to examine the responses of the plant to clipping treatments in different stages of its life cycle and, also, to determine moisture and dry matter production. In each clipping stage the carbohydrate of both roots and aerial parts of the plants were determined.

Plants were clipped during the years of 1969 and 1970 using two height treatments:

a. 0 percent (check), and

b. 100 percent clipping.

Plants were clipped at four stages of development:

1. rosette,
2. bolting,
3. flowering, and
4. seed setting.

At each stage four plants were harvest and analyzed for moisture content, dry matter production, and carbohydrate content of aerial parts. Also, two plants were examined for root development and root carbohydrate content.

After each cutting treatment plants were observed weekly to see the reaction to the cutting and to clip again if necessary. At the end of the year a number of clippings were made for each treatment.

Carbohydrate determinations were done following a modified Weinmann method of removing total nonstructural carbohydrates as described by Smith (1969). Duplicate determinations were run of each sample prepared through the standard procedure as described by the same author.

Chemical Analysis

Samples of *Rudbeckia* were sent to the Industrial Laboratories Company, Denver, Colorado, for chemical proximate analysis when the plants were at bolting stage. The sample was a composite of the entire aerial portion.

Toxicity Studies

To determine whether *Rudbeckia* produces symptoms of poisoning to livestock 400 pounds of green material from the field were collected in seed set stage the last week of August, 1970. This stage coincides with the dates that the Forest Service allows grazing in the area. The material was dried and ground and, in cooperation with the U. S. D. A. Poisonous Plant Research Laboratory at Logan, three sheep were fed by pumping into the rumen during the first day of the trial 1 pound, 2/3 and 1/2 pound of ground material, respectively. The second day the doses for the 1/2 and 2/3 pound were raised to 1 1/3 pounds each, and it was followed, in that way, for 4 days to see whether symptoms of poisoning by *R. occidentalis* occurred.

RESULTS AND DISCUSSION

Taxonomy and Morphology of Rudbeckia occidentalis

The distribution of R. occidentalis in the Intermountain Region is shown in Figure 3.

Records of the species collected at different sites of the Intermountain States as found in herbaria of the Utah State University and University of Utah are shown in the Appendix III.

R. occidentalis grows from the ponderosa pine zone up to and including the spruce zone, usually in moist but not saturated soil, and sometimes in moderately dry, poor, shallow soil. Throughout most of its range it grows as scattered plants. Occasionally it covers a few hectares densely and in certain localities it may be abundant over extensive areas. The species is perhaps most common in Utah where it is fairly prevalent throughout the aspen zone. Tidestrom (1925) reported R. occidentalis to occur in the yellow pine, aspen and spruce belts from Wyoming and Utah westward to Washington and California.

Description of the species

Rudbeckia occidentalis Nutt. (Trans. Am. Phil. Soc., 1840) is a coarse perennial herb of the aster or sunflower family. It is sometimes called "Niggerhead" or "Western coneflower," the specific name occidentalis meaning western, and the flower head being conspicuously cone-shaped.

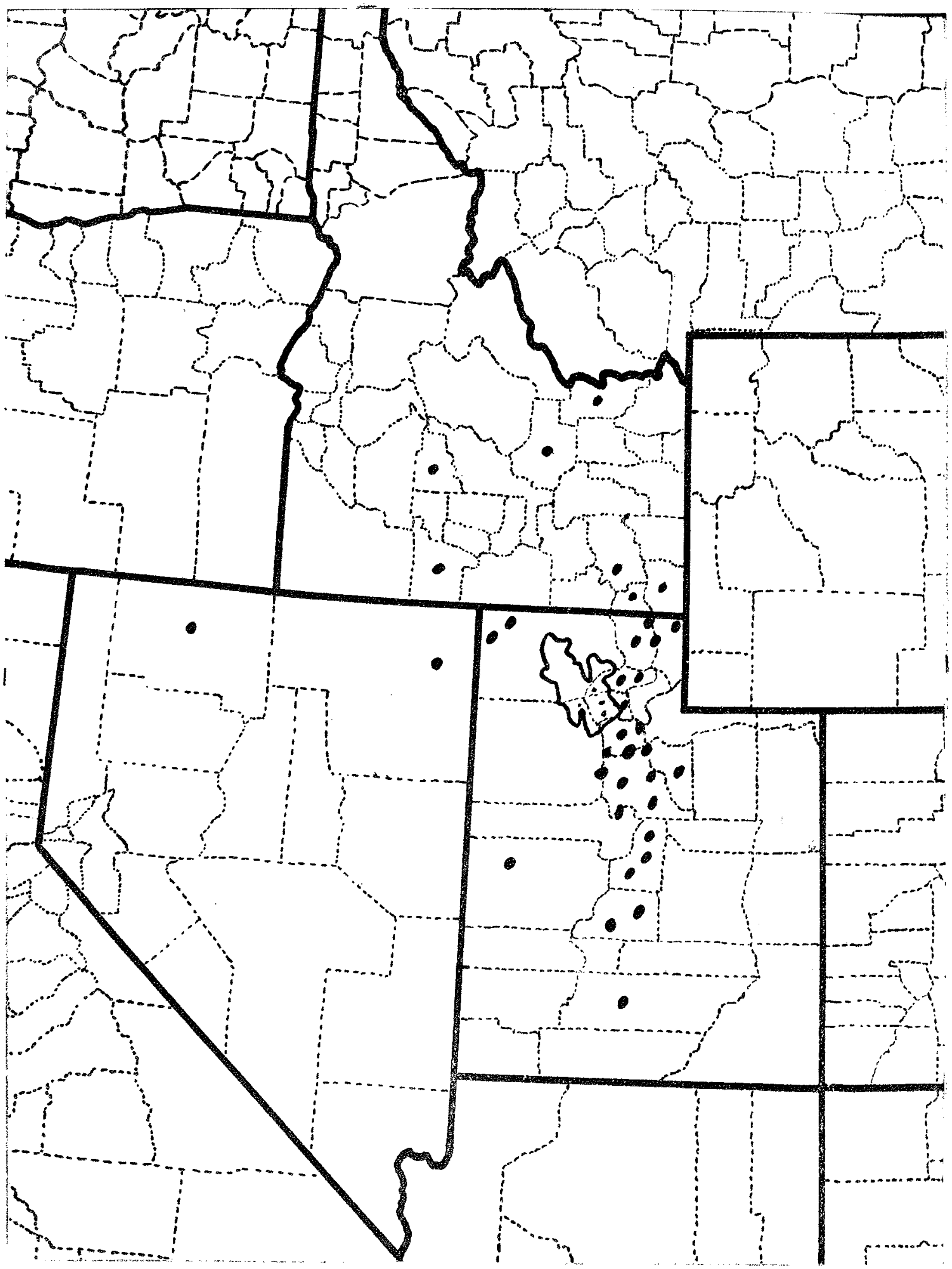


Figure 3. Distribution of Rudbeckia occidentalis in the Intermountain region.

Roots are coarse, woody, fibrous, from a thickened, much-branched and distorted crown which often attains a diameter up to 30 or 60 cm in the older plants. Stems are stout, occasionally 2.50 m high, nearly glabrous, ridged, often clustered at base, usually simple. The leaves are alternate, simple, ovate, acuminate at apex, mostly rounded or somewhat cordate at base, entire or irregularly and sparingly toothed glabrous of minutely rough-hairy; 1 to 10 cm wide, 1 to 20 cm long; lower leaves stalked, the stalks wing-margined; upper leaves sessile. Involucral bracts grow in a series surrounding the base of the flower head, imbricate, usually in 2 rows, leaf-like, oblong or lanceolate, up to nearly 3 cm long, spreading. Inner or upper (disk) flowers of the head-numerous, brownish to purplish, short-tubular, perfect, seed-producing, each with a chaffy bract (palea) loosely clasping it; outer (ray) flowers of the head absent. Flower heads appear short-conic to columnar, usually solitary, on long stalks at ends of stems or stem branches, these heads start as small buttons, which gradually elongate until at blossoming time, they attain full growth and may then become 5 cm long. Seeds (achenes) are thickened, somewhat angled, each tipped by a white-papery, short but deeply and minutely toothed, persistent crown. Seed size is approximately 1 to 3 mm wide, and 3 to 8 mm long.

Marked variations in size of the plant and its parts may occur due to site conditions.

Phenology

Mature plants

Growth of mature plants of R. occidentalis begins as soon as snow melts and with continually rising average temperature. In 1969 the rosette stage was attained on May 29, the first stage of the life cycle of coneflower. In 1970 the same stage was attained on June 11, almost 13 days later. The condition of late snow melt and associated low temperature created a time lag of about 2 weeks. Temperature appears to constitute a limiting factor for the rosette stage.

The rosette stage is characterized by a whorl of leaves ranging in number from 6 to 50 leaves per plant, depending on the size of the rosette. In marked plants, the average numbers was 8.5 for 1969 and 10.32 for 1970 (Figure 4 and Table 10).

Figure 4. Plant of R. occidentalis at the rosette stage.

Table 10. Number of stems, leaves per stem, and leaf measurements from rosette to seed setting stage in *Rudbeckia occidentalis*, 1969 and 1970

Dates[a]								
5-22 6-11	5-29 6-18	6-6 6-25	6-20 7-2	7-3 7-9	7-12 7-16	7-18 7-23	7-29 7-30	8-14
Average number of stems from rosette to seed setting stage								
7.4	8.0	7.2	7.7	7.7	7.7	7.6	7.5	Dry
	9.2	9.0	9.0	8.8	8.8	8.7	8.5	
Average number of leaves per stem from rosette to seed setting stage								
8.5	13.55	13.83	11.82	11.83	11.90	13.75	17.15	Dry
10.32	15.15	15.83	13.21	13.20	13.01	13.00	12.85	
Average width of leaves in the middle of the stems from rosette to seed setting								
4.38	5.66	6.64	8.77	8.80	8.85	9.69	10.10	Dry
5.17	5.72	6.81	7.55	7.83	7.90	8.70	9.15	
Average length of middle leaves from rosette to seed setting								
6.85	12.02	14.86	17.33	17.80	17.85	15.57	16.38	Dry
6.20	12.00	13.05	15.65	15.85	16.50	16.93	16.78	

[a] First line in each category is 1969, second line in each category is 1970.

With increasing temperature, the next stage (bolting) was rapidly attained, and occurred after one week during 1969 and 1970. This stage was mainly characterized by a rapid growth of the stems at a rate of 3.66 cm daily for 1969 and 3.86 cm for 1970, the highest rate of growth for the entire cycle of coneflower (Figure 5). Maximum average stem height was 24.3 percent higher in 1970 than in 1969 (Figure 6). This may be attributed to the late snow that fell in 1969 when the plants were in the bolting stage, bending the stems and producing an abnormal growth.

By July 18, 1969, and July 23, 1970, 10 percent of the heads of "coneflower" had their flowers opened, and almost 1 week later, 50 percent of the flowering was attained, with 100 percent flowering reached on July 28, 1969, and August 13, 1970. The sequence of individual flower development around the cone is upward, the lower part of the cone flowering first.

The flowering stage is characterized by the presence of the flower head, which usually has a short conic to columnar form and develops solitarily on long peduncles at the end of stems or stem branches. Usually apical dominance is present (Figure 7). After the flowers are in anthesis cross-pollination is the principal mechanism for seed setting and is done principally by bees. The results of pollination studies in flowers covered with cloth bags before pollination and plants without bags show 97 percent cross-pollination. Seed germination tests on seeds from two different sources (Table 11) confirm results of the flower bagging experiment.

The seed-setting stage was initiated by August 14, 1969, and August 20, 1970, almost a lag of 1 week between 1969 and 1970. By August 25, 1969, and

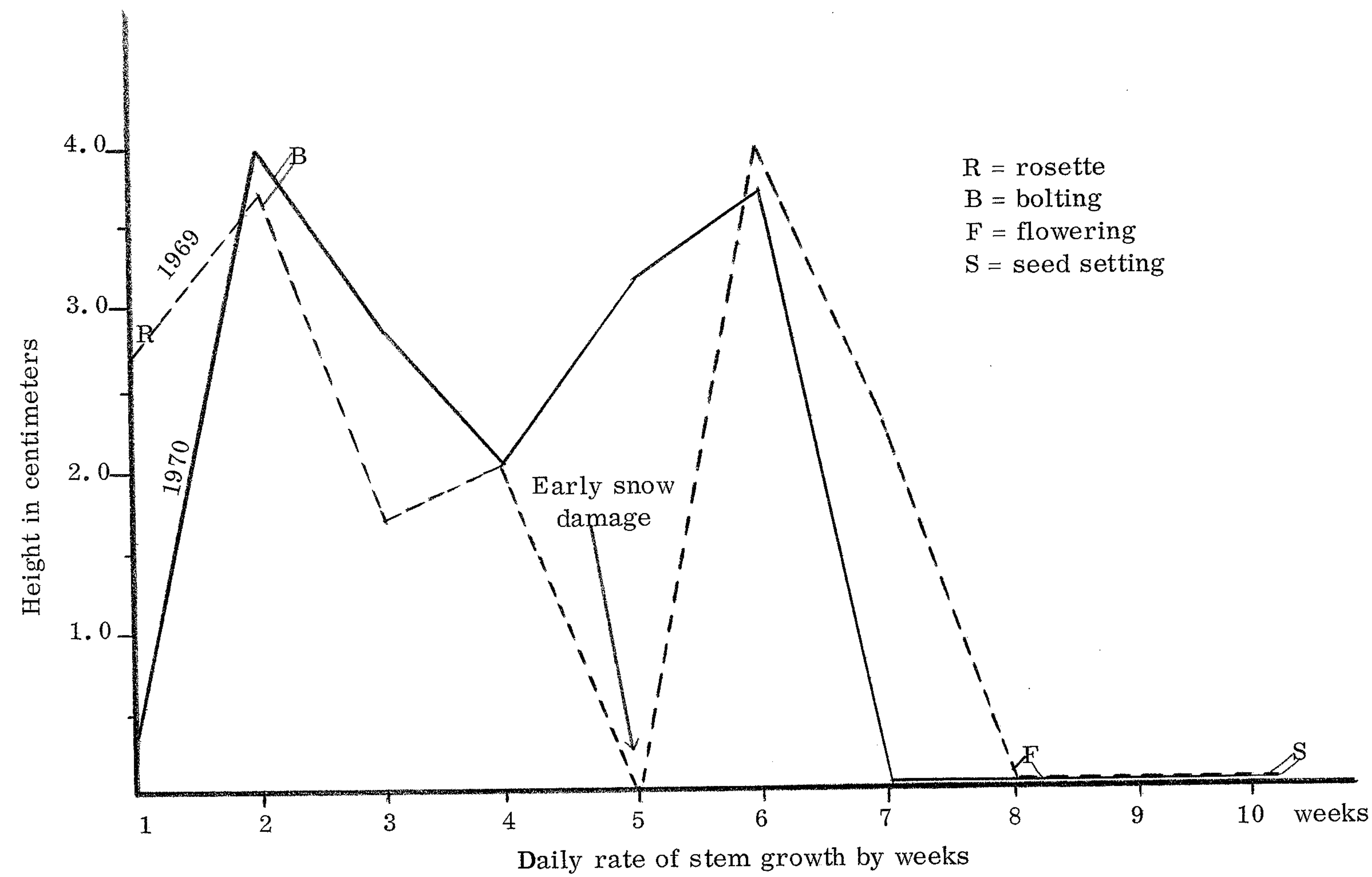


Figure 5. Rate of stem growth of Rudbeckia occidentalis from rosette to seed setting stages. From: May 22 to August 14 for 1969, June 11 to August 20 for 1970.

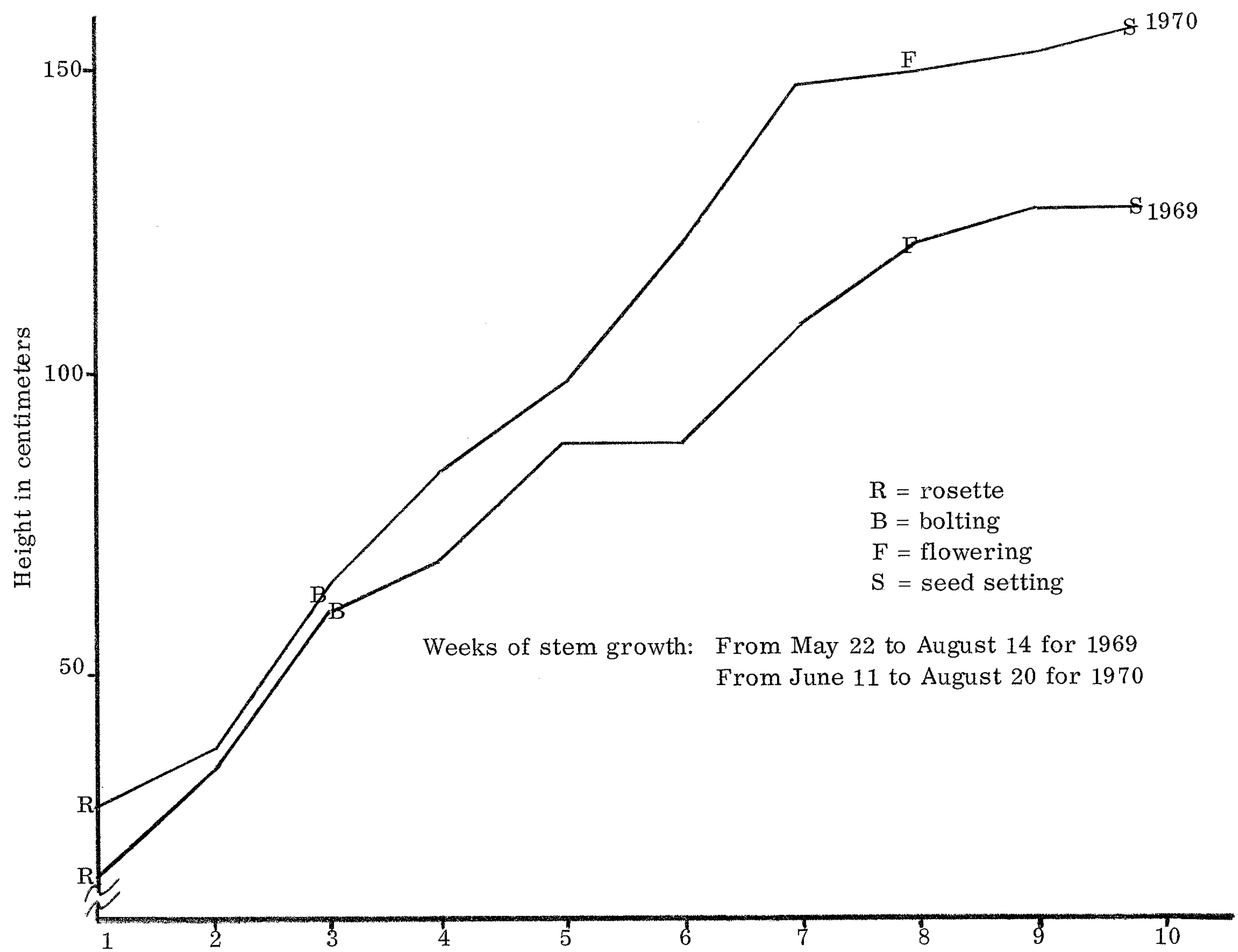


Figure 6. Stem growth of Rudbeckia occidentalis by weeks from rosette to seed setting stage.

Figure 7. Cone of R. occidentalis at the flowering stage. Individual flowering take place upward in the cone.

Table 11. Seed germination results of plants prevented from cross-pollination and plants cross-pollinated

Year	Replication No.	Percent germination	
		Cross-pollinated	Self-pollinated
1969	1	87	3
	2	87	4
	3	88	2
	4	89	3
	5	88	2
	Average	88 a *	2.8 b
1970	1	76	3
	2	80	3
	3	78	1
	4	78	4
	5	77	3
	Average	78 a	2.8 b

*Means followed by different letters are significantly different at the 5 percent level as determined by the Duncan Multiple Range Test.

August 30, 1970, all the plants with heads completed the seed formation process. Dissemination was started at this time and was completed by September 15 and 17 during both years (1969, 1970).

In Table 12 are presented different aspects of the "cone" characteristics and their number of seeds. In each stem there is usually one principal "cone or head" accompanied by a few secondaries. The average number of heads on 200 plants was 2.78. The average number of seeds per head was 588 with a 36 percent viability.

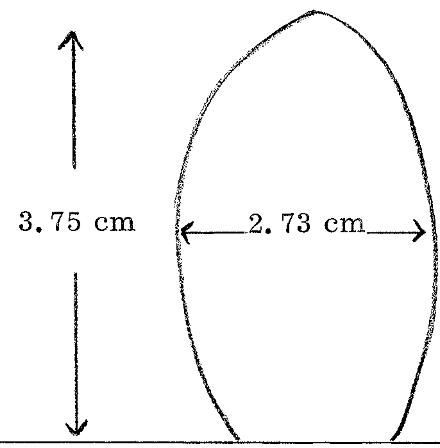
Plant height and cone size are different for plants growing under aspen shade or in open areas. Measurements of 250 plants in each area, showed that the average maximum height of a plant under shade condition was 1.40 m and in open conditions 1.09 m, a difference statistically significant according to the Duncan test. Also, the average length of the cone was significantly larger under shade than in open areas. However, even though the diameters of the cones were slightly larger under shade than in open conditions, this difference was not statistically significant (Table 13).

A complete phenological calendar of the life cycle of *R. occidentalis* is presented in Table 14.

Seed dissemination

Dissemination of "coneflower" seeds is mainly by gravity but the distribution around the mother plant depends entirely upon the wind action. Therefore, direction of dissemination when wind is the agent is influenced by the intensity of wind and the direction. Daubenmire (1959) said that in forest

Table 12. Average cone measurements and number of seeds per head of Rudbeckia occidentalis



Average number of cones per stem: 2.78,
including one principle head.

Average number of seeds per head: 588

Average number of viable seeds: 211 36 percent

Head measurement:

Diameter range: 2.00 to 3.00 cm

Length range: 2.50 to 5.00 cm

Average diameter: 2.73 cm

Average length: 3.75 cm

Table 13. Average measurements in centimeters of heads and plant heights, from 250 plants in each area, in open and shade conditions (stage of growth--50 percent flowering)

Averages	Open	Shade
Head		
Length	3.00 b *	4.13 a
Width	2.45 a	2.78 a
Height of plants	109.36 cm b	146.00 a
Diameter range	2.0-3.0	2.5-3.0
Length range	2.0-4.0	3.5-5.0

*Means followed by different letters are significantly different at the 5 percent level as determined by the Duncan Multiple Range Test.

Table 14. Phenology of Rudbeckia occidentalis during two different years

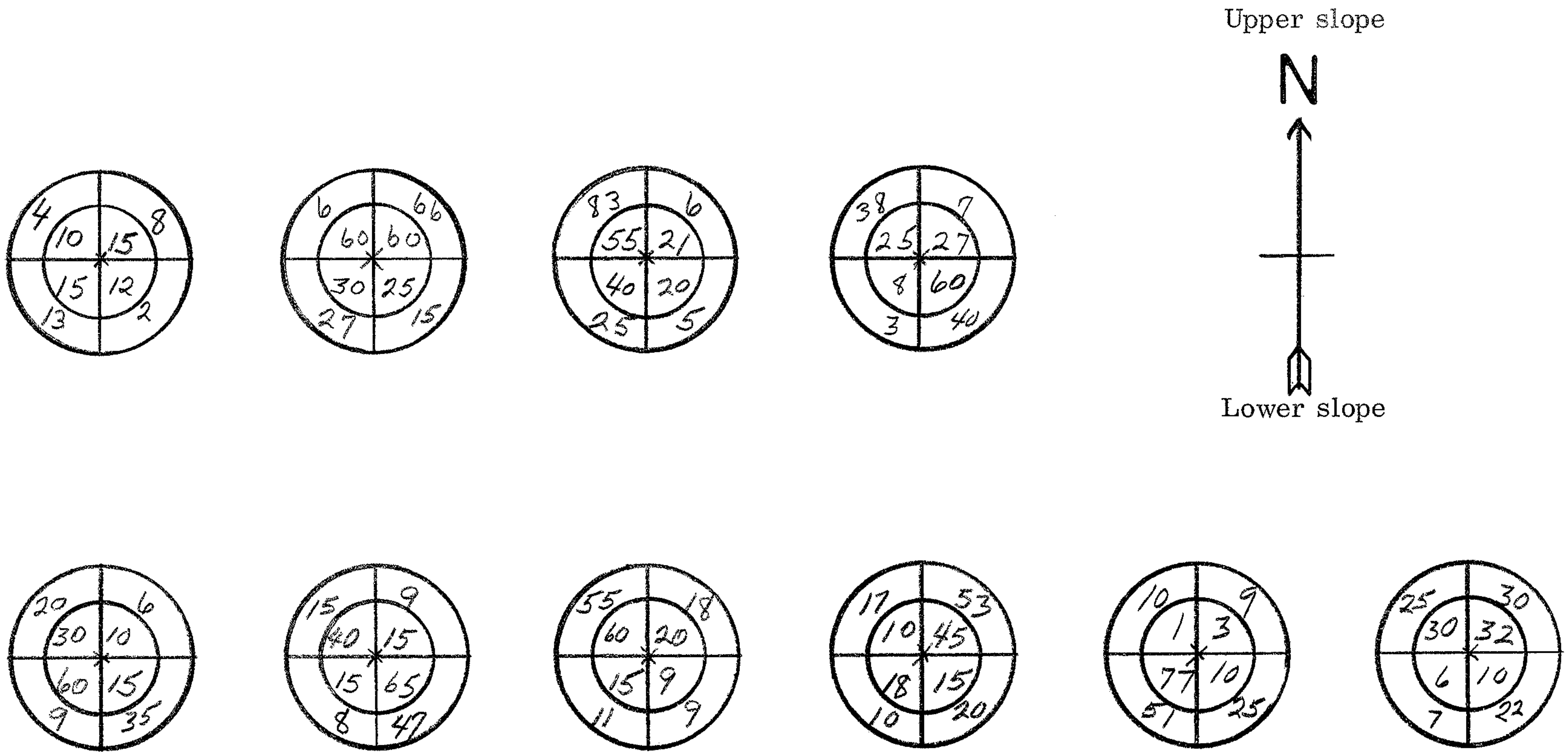
Phenological stage	1969	1970
Rosette development completed	May 29	June 11
Bolting development completed	June 6	June 18
Flowering initiated	July 18	July 23
Flowering 50 percent completed	July 23	August 5
Flowering 100 percent completed	July 28	August 13
Seed setting initiated	August 14	August 20
Seed setting completed	August 25	September 3
Dissemination initiated	August 20	August 30
Dissemination completed	September 15	September 17

vegetation anemochory is significantly more prevalent among the trees, and relatively uncommon among the undergrowth plants that live in a microclimate with little wind movement. In the case of "coneflower" dissemination, it is the little wind movement and maybe the action of birds and mammals responsible for the movement of the stems of Rudbeckia, causing the seeds to be shaken out as they mature when the cone is buffeted by the wind. This is the reason why seeds of "coneflower" show no discernible pattern of distribution around the mother plant. In some cases there are more seeds down the slope but in others there are more up the slope. The results of dissemenation studies in 1969 and 1970 were similar and show the characteristics described above although in most of the plants studied the seeds were more prevalent in the inner circle than in the outer one (Figure 8).

Root studies

The root appears to function efficiently as an organ of anchorage and absorption and, also, as an organ of storage. Apparently the root has regenerative characteristics in the form of root sprouts which give origin to new plants near the mother plant and which become independent after a time.

The nature of the root system appears to be considerably influenced by edaphic influences such as texture, aeration, moisture and presence or absence of indurated layers. Depth of penetration is not great, since it was found that the soil may be penetrated by roots to between 25 cm and 120 cm.



×Location of the mother plant

Figure 8. Seed dissemination of Rudbeckia occidentalis in four plants for 1969 and six plants for 1970.

The roots of "coneflower" are so variable that it is difficult to describe them with a simple term or phrase. It is apparent that the habitat in which the root develops has considerable influence upon its morphology. Two characteristics are noteworthy. One is the apparent ability of the root to penetrate indurate layers by slow vertical extension. The second is extensiveness which allows the plant to draw upon a large volume of soil. Examination of roots from mature plants showed a tendency for the roots to concentrate above a depth of 80 cm in the soil of the study area.

Good root development is also attained in soils with acid reaction. In soils with high pH the roots are less vigorous and as a consequence so is the entire plant. In greenhouse conditions addition of lime to the soil resulted in plants that were about 30 percent shorter in height than plants growing with a pH of 5.5 (Figure 9).

Figure 9. Response to lime application of two plants of Rudbeckia occidentalis growing in soil from the study area. Left plant with lime application, right plant check.

Seedlings

The total density of seedlings alive at particular times of the year when determinations were made is an indication of how favorable the previous environmental conditions were. In both 1969 and 1970 the mean density of seedlings of "coneflower" alive in both exclosures decreased as the season advanced (Tables 15 and 16). This decrease in seedling survival reached the maximum value during the period of June 20 to July 12 in 1969 and from June 18 to June 25 in 1970 (Figure 10) and was probably due to the competition produced by the rapid growth of the associated species, particularly mature plants. Also, climatic conditions have a great influence on survival of seedlings as in 1969 when a late snow produced an increase in the seedling mortality at the end of June.

Table 17 shows the density per m^2, percent cover, percent frequency, and square cm of basal area made along transect No. 1 (lower) and No. 2 (upper) where the seedling studies were done. To clarify the relative importance of the various species the relative density, relative dominance and relative frequency were calculated (Table 18). The addition of these three values for each species provides and index described as "important value" by Cain and Castro (1959) which allow us to see that the two most important species associated with the seedlings of coneflower in the area are mountain brome grass and mature plants of "coneflower." It is this abundance, especially of "coneflower," which produce the biggest competition for seedling development. This is particularly true when the mature plants go from

Table 15. Growth and development of _Rudbeckia occidentalis_ seedlings during 1969 (averages of 100 plants measurements)

Date									
6-9	6-20	7-3	7-12	7-18	7-29	8-14	8-25	9-5	9-12
Average height measurements in centimeters									
3.22	4.44	4.98	5.61	6.88	6.93	6.13	6.61	6.50	4.85
Average number of leaves per seedling									
3	3	2.5	2.2	2.5	2.8	2.8	3.0	3.0	2.0
Average width of leaves in centimeters									
1.27	2.11	1.75	2.71	2.35	3.83	2.57	3.13	3.15	3.50
Average length of leaves in centimeters									
1.91	3.10	2.63	1.98	3.68	2.59	3.53	3.73	3.80	2.41
Seedling survival in percentage									
100	99	89	65	63	60	58	55	53	51
Stem/root weight ratio									
1:1	1:1.3	1.4:1	1.7:1	1.5:1	1.3:1	1.1:1	1:1.23	1:1.17	1:2.5
				1 bud	1 bud	2 buds	2 buds	3 buds	3 buds

Table 16. Growth and development of Rudbeckia occidentalis seedlings during 1970 (averages of 100 plants measurements)

Dates									
6-11	6-18	6-25	7-2	7-9	7-16	7-23	7-30	8-13	8-20
Average height measurements in centimeters									
4.75	4.78	4.90	5.80	7.10	7.40	7.30	7.32	7.17	5.61
Average number of leaves per seedling									
3	2.6	2.5	2.5	2.6	2.9	3.0	3.0	2.75	2.70
Average width of leaves in centimeters									
2.31	2.40	2.43	2.50	2.61	2.87	3.17	3.48	3.71	3.68
Average length of leaves in centimeters									
3.17	3.19	3.10	3.25	3.52	3.49	3.80	3.75	3.76	3.70
Seedling survival in percentage									
100	98	72	71	68	65	64	64	61	60
Ratio weight of stem and root									
1:1.1	1.2:1	1.8:1	2.0:1	1.87:1	1.70:1	1.17:1	1.0:1.15	1:1.36	1:1.38
			1 bud	1 bud	2 buds	2 buds	3 buds	3 buds	3 buds

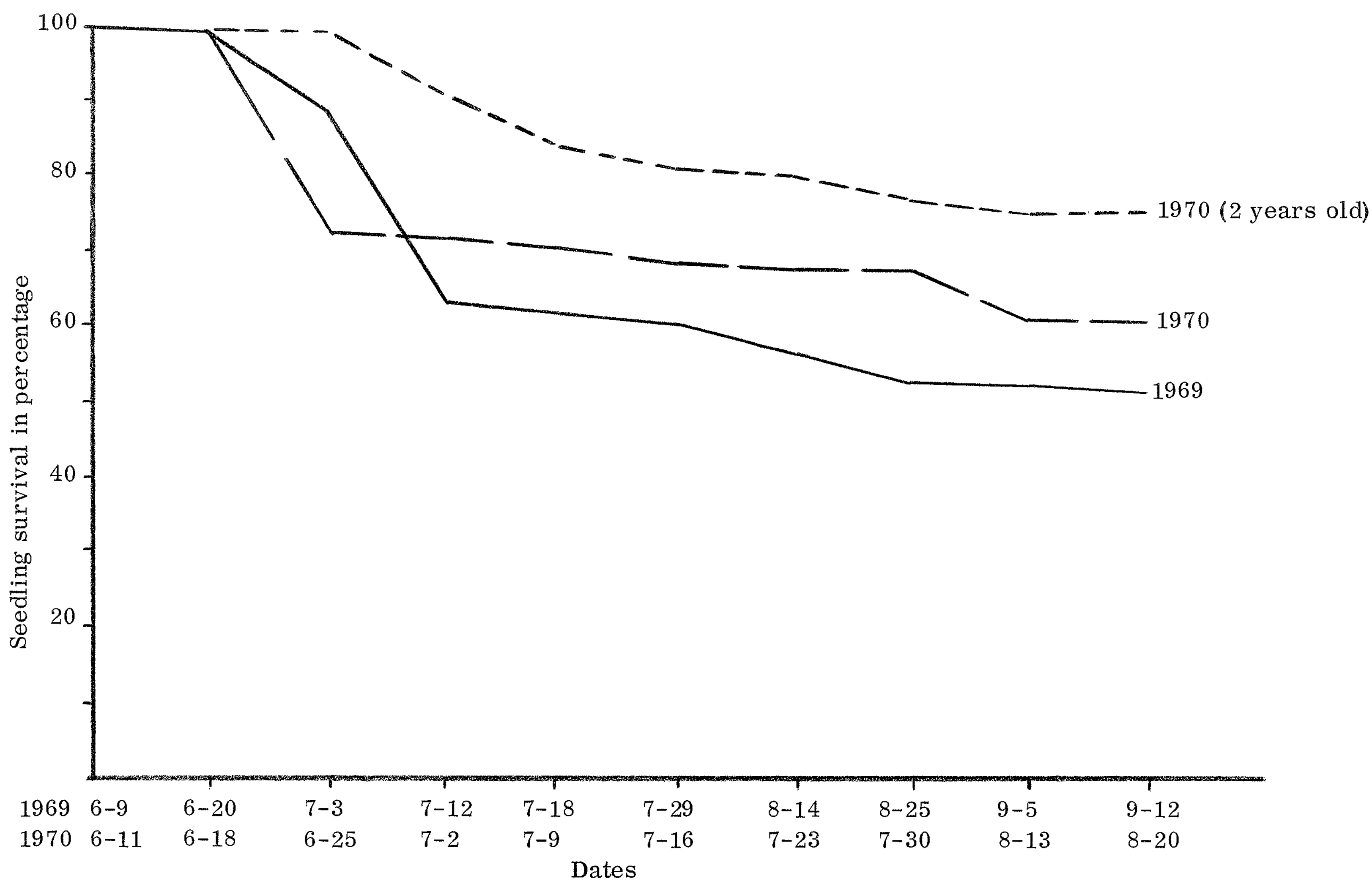


Figure 10. Seedling survival of Rudbeckia occidentalis during 1969 and 1970 for 1 year old plants and during 1970 for 2 year old plants.

Table 17. Vegetation analysis of two transects for seedling studies of *Rudbeckia occidentalis*

Species name	Lower: Density m^2	Lower: Cover %	Lower: Basal area cm^2	Lower: Frequency %	Upper: Density m^2	Upper: Cover %	Upper: Basal area cm^2	Upper: Frequency %
Symphoricarpos oreophilus					1.81	3.69	19.69	25.0
Sambucus racemosa	1.31	6.88	7.19	25.0	1.38	6.56	12.19	25.0
Rudbeckia occidentalis	30.25	20.63	76.69	100.0	16.25	11.25	58.31	100.0
Senecio serra	0.13	0.31	1.56	6.25	1.31	1.94	6.88	37.50
Agastache urticifolia	0.84	0.69	1.62	18.75	1.88	0.69	5.31	43.75
Hackelia floribunda	0.44	0.63	15.63	12.50	0.44	0.25	1.25	12.50
Vicia americana					0.44	0.06	0.38	12.50
Delphinium occidentale	0.13	0.19	0.62	6.25				
Bromus polyanthus	27.68	5.93	113.94	100.0	27.63	12.81	119.69	100.0
Agropyron trachycaulum	T			6.25	2.69	1.13	14.38	43.75
Poa reflexa	T			6.25	T			6.25

Table 17. Continued

	Plot location							
	Lower				Upper			
Species name	Density m^2	Cover %	Basal area cm^2	Frequency %	Density m^2	Cover %	Basal area cm^2	Frequency %
Elymus glaucus	2.94	1.69	25.0	56.25	1.31	0.56	5.63	50.0
Carex occidentalis	T			6.25				
Collomia linearis	0.38	0.13	0.38	87.50	T			43.75
Chenopodium album	0.31	0.13	0.13	75.0	T			87.50
Polygonum douglasii	11.12	1.94	2.31	81.25	T			87.50
Phacelia utahensis	2.50	1.19	8.25	50.0	3.06	1.94	10.0	68.75
Stellaria jamesiana	1.00	0.06	0.31	31.25	T			12.50
Balsamorhiza sagittata	0.13	0.06	0.06	6.25				
Smilacina racemosa	0.25	0.13	0.50	6.25	1.56	0.62	1.25	6.25
Total	79.51	40.59	254.19	681.25	59.76	41.50	254.96	762.50

rosette to bolting stage resulting in increase of 100 percent in the plant cover.

At the end of the growing season in 1969 51 percent of the seedlings were alive, in contrast with 1970 when 60 percent were alive. The difference is mainly the effect of a late snow in 1969. In both years seedling growth was restricted to the development of one stem which reached an average height of 4.85 cm for 1969 and 5.61 cm for 1970. During both periods only one to three leaves were developed in the stem with average maximum leaf measurements at the end of the season of 3.50 cm in width, 3.80 in length for 1969 and 3.71 in width and 3.80 in length for 1970. However, even the seedlings do not develop very much during their first year and remain small. The shoot/root weight ratio is a good indication that the main development during this stage of life is in the root. From a ratio of 1 to 1 at the beginning of the season the ratio increased from 1 to 1.25 at the end of 1969 and from 1 to 1.38 at the end of the 1970 growing season. Also, at this point it is possible to observe in the crowns the development of three buds which will be the regrowth during the next year after snow melt (Tables 15 and 16).

In 1970 only 40 seedlings from the total possible 49 remaining from 1969 were found after snow melt for a second year of study.

These seedlings showed a different behavior than in their first year of growth (Table 19 and Figure 11). The average height measurement increased in heigh from 10.1 cm at the beginning of the season (June 11) to a maximum of 22.10 cm on July 9. The average number of leaves also was greater, reaching a maximum of 3.6 per plant. The average maximum leaf width was 6.01 cm

Table 18. Relative density, relative dominance, relative frequency and importance value of the vegetation of two transects for seedling of Rudbeckia occidentalis studies

Species name	Plot location							
	Lower				Upper			
	Relative frequency	Relative density	Relative dominance	Importance value	Relative frequency	Relative density	Relative dominance	Importance value
Symphoricarpos oreophilus					3.28	3.03	7.72	14.03
Sambucus racemosa	3.66	1.65	2.83	8.14	3.28	2.31	4.78	10.37
Rudbeckia occidentalis	14.68	38.06	30.17	82.91	13.11	27.19	22.87	63.17
Senecio serra	0.92	0.17	0.61	1.70	4.92	2.19	2.69	9.80
Agastache urticifolia	2.75	1.18	0.64	4.57	5.74	3.14	2.08	10.96
Hackelia floribunda	1.83	0.55	6.15	8.53	1.64	0.74	0.49	2.87
Vicia americana					1.64	0.74	0.16	2.54
Delphinium occidentale	0.92	0.16	0.24	1.32				
Bromus polyanthus	14.68	34.81	44.82	94.31	13.11	46.23	46.94	106.28
Agropyron trachycaulum	0.92			0.92	5.74	4.50	5.64	15.88
Poa reflexa	0.92			0.92	0.82			0.82
Elymus glaucus	8.26	3.69	9.84	21.79	6.55	2.19	2.22	10.96
Carex occidentalis	0.92			0.92				
Collomia linearis	12.84	0.47	0.15	13.46	5.74			5.74
Chenopodium album	11.00	0.38	0.05	11.43	11.47			11.47
Polygonum douglasii	11.93	13.99	0.91	26.83	11.47			11.47
Phacelia utahensis	7.34	3.14	3.25	13.73	9.03	5.12	3.92	18.07
Stellaria jamesiana	4.59	1.26	0.12	5.97	1.64			1.64
Balzamorhiza sagittata	0.92	0.17	0.03	1.12				
Similacina racemosa	0.92	0.32	0.19	1.43	0.82	2.69	0.49	3.93
	100.00	100.00	100.00		100.00	100.00	100.00	

Table 19. Growth and development of *Rudbeckia occidentalis* seedlings in their second year of growth, 1970 (average of 40 plants)

Dates									
6-11	6-18	6-25	7-2	7-9	7-16	7-23	7-30	8-13	8-20
Average height measurements in centimeters									
10.1	11.25	12.10	16.30	20.10	22.10	22.07	20.75	20.15	20.12
Average number of leaves per seedling									
3.0	3.0	3.1	3.15	3.60	3.50	3.40	3.47	3.40	3.13
Average width of leaves in centimeters									
2.45	3.17	3.85	4.00	5.12	5.11	5.13	6.01	5.95	5.81
Average length of leaves in centimeters									
5.20	5.29	6.10	6.15	7.75	7.60	7.42	7.40	7.41	7.40
Seedling survival in percentage									
100	99	98	90	85	82	80	77	75	75
Ratio weight of stem and root									
1:1.4	1:1.8	1:1.90	1:2.10	1:2.20	1:3.10	1:3.15	1:3.20	1:3.18	1:3.27

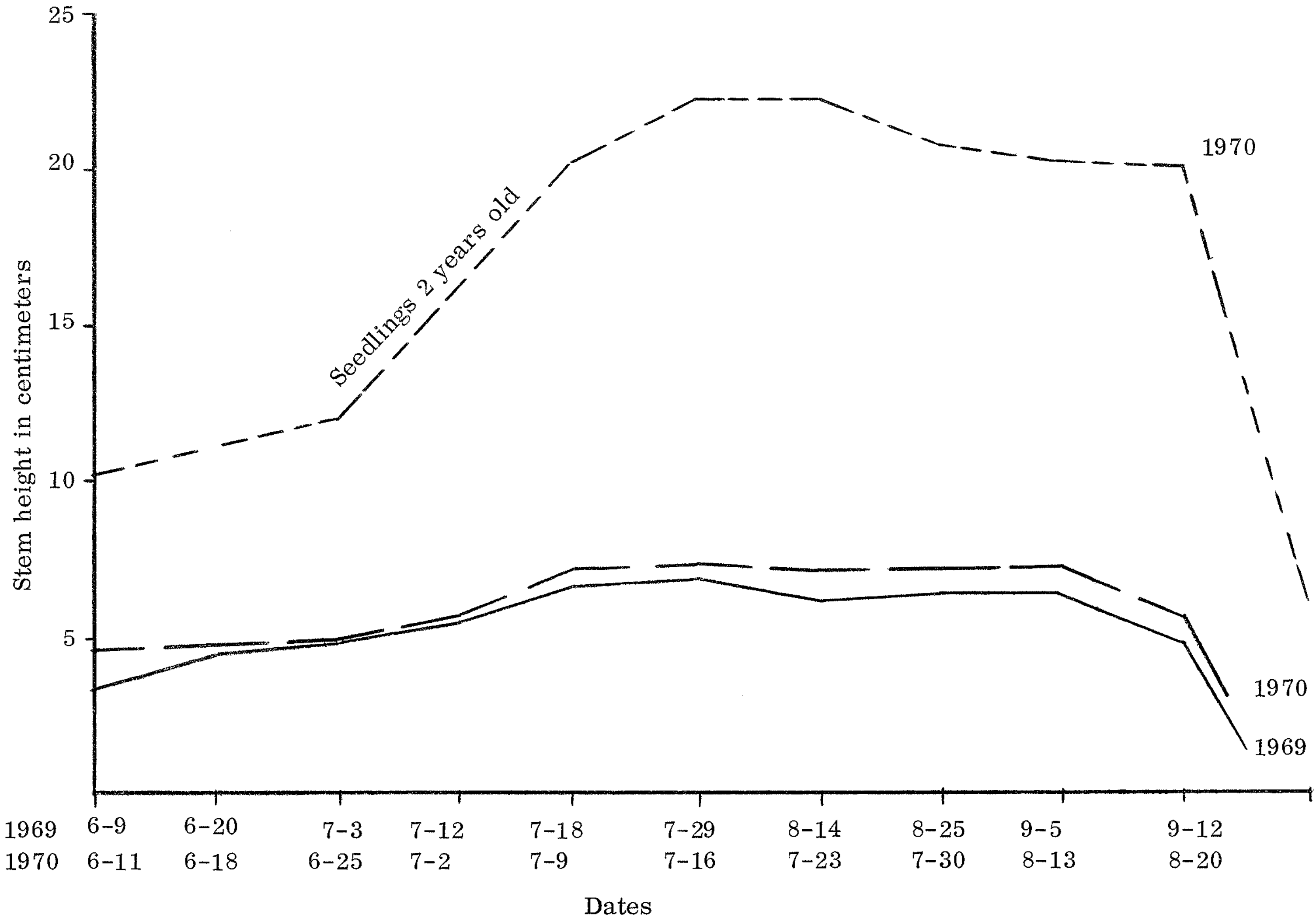


Figure 11. Growth and development of Rudbeckia occidentalis seedlings 1 year old (1969 and 1970) and 2 years old (1970).

while the average maximum length was 7.75 cm. At the end of the season the survival percentage was 75, higher than in the first year. Also the root attained a greater development, reaching a shoot/root weight ratio of 1 to 3.27. At this stage of the life cycle of coneflower the plants still maintained their rosette form without bolting. In seedlings with more development and 3 years of age it was possible to see bolting develop but in general only plants 4 years old began bolting, flowering and seed production. The first 3 years of growth is devoted to good root and bud development.

During the winter months when up to 2 meters of snow are on the ground, no growth was detected in any seedling or mature plants. Growth started as soon the temperature was high after snow melt (Figure 12).

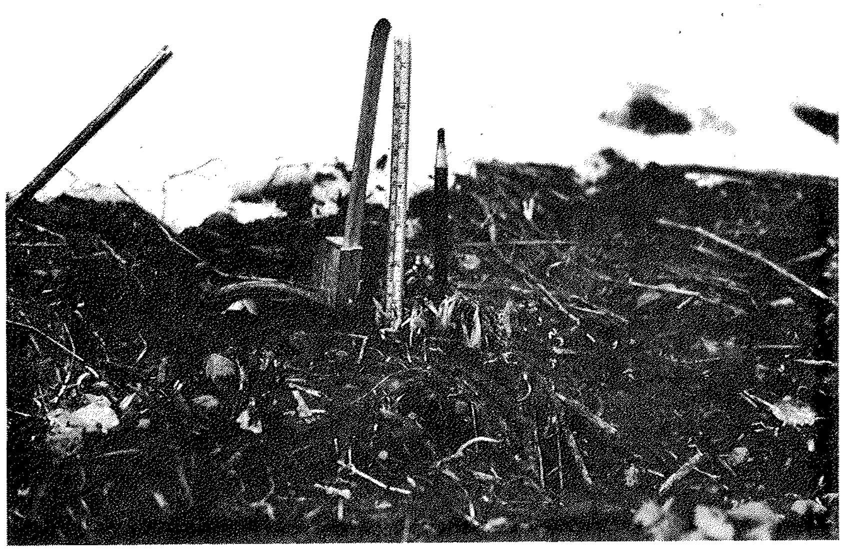


Figure 12. Germination of Rudbeckia occidentalis plants as soon as snow melts.

Seeds

Seeds of R. occidentalis collected from the Tony Grove area during August of 1968 were subject to the influence of different temperatures and photoperiods in germination tests using two growth chambers during March of 1969.

Seeds of various size of "coneflower" gave no statistically significant differences in germination results under the temperature and light treatments indicating that size is not important in the germination of this species and that large seeds germinate as easily as small seeds under optimum conditions (Table 20).

When seeds were subjected to temperature treatments the results showed that alternating temperatures produce higher germination percentage than constant temperature. So, treatments at alternating temperatures of 25 C-15C or 15 C -5C and light conditions produce an average of 92 and 79 percent of germination in contrast to an average of 52 percent for room condition (relatively constant temperature of 23 C $\pm$ 2 and room light conditions). In contrast, alternating temperatures under dark conditions gave significantly lower germination percentage than under room conditions (Table 20) where an average germination percentage for the two alternating temperatures studies were 27 and 52, respectively. Therefore, light is required for optimal germination of seeds of R. occidentalis.

Under the same photoperiod (8 hours light) the higher alternating temperatures (25 C-15 C) gave statistically significant higher germination

Table 20. Seed germination results of Rudbeckia occidentalis under two treatments of alternate temperature and one of constant temperature, two light treatments and two seed sizes

		Temperature				
		25 C (8 hr.)- 15 C (16 hr.)		15 C (8 hr.)- 5 C (16 hr.)		
Seed		Light		Light		Room condition
size	Rep.	8 hr.	Dark	8 hr.	Dark	23 C $\pm$ 2
Large	1	92	32	68	52	52
	2	94	20	72	52	52
	3	93	27	88	51	64
Small	1	92	24	88	52	57
	2	90	36	80	52	52
	3	92	26	81	53	60
Average		92.1	27.5	79.5	52	66.1

Duncan Test:

Large versus small seeds = Not significant.
25 C-15 C Temperature versus 15 C-5C = Significant.
25 C-15 C Temperature, 8 hours light versus 25 C-15 C Temperature, dark = Significant.
15 C-5 C Temperature, 8 hours light versus 15 C-5 C Temperature, dark = Significant.
25 C-15 C Temperature, 8 hours light versus Room Condition = Significant.
15 C-5 C Temperature, 8 hours light versus Room Condition - Significant.

percentages over the lower alternating temperatures (15 C-5 C) as we can see in Table 20 where the averages are 92 percent and 79 percent, respectively.

The same alternate temperatures under dark conditions produce reverse results; 52 percent germination for 15 C-5 C and 27 percent for 25 C-15 C, a result of the temperature-light interaction on the interaction on the germination of "coneflower."

From the results of this experiment we can conclude that the higher alternating temperature of 25 C015 C and 8 hours light are required for optimal germination of seeds of R. occidentalis.

The percentage of filled seeds in heads reflects how favorable the conditions were after the flowers were pollinated. This could be related to the moisture availability during the post-pollination period to the availability of nutrients to the plant from the soil, to the translocation from the plant to the seed, to the temperature during this period, or to other factors. In order to determine the magnitude of these influences on different sites in Utah seeds from individual plants were collected in different places (Table 21) during 1969 and also during 1970 (Table 22). The results showed large differences in percent germination among places. These differences are difficult to explain with the limited knowledge available within this study. However, it appears that altitudinal effects are important in the production of viable seeds (Table 23) where seeds from high altitude at Ephraim (10,400 feet) had very low germinations, 1.33 and 0.0 percent in comparison with seeds from

Table 21. Results of germination of seeds collected from one plant of _Rudbeckia occidentalis_ at different locations within the State of Utah, 1969

Source	Date collection	Replication	Percent germination	Average
Ephraim--under aspen (10,400 feet)	8/27/69	1	0	1.33
		2	0	
		3	4	
Ephraim--under aspen (8,800 feet)	8/29/69	1	48	44.0
		2	52	
		3	32	
Ephraim--under aspen (8,800 feet)	8/27/69	1	44	46.6
		2	56	
		3	40	
Ephraim--open (10,400 feet)	8/27/69	1	0	0.0
		2	0	
		3	0	
Mud Creek--open (8,000 feet)	9/8/69	1	92	88.0
		2	92	
		3	80	
Mud Creek--open (8,000 feet)	9/8/69	1	80	65.3
		2	64	
		3	52	
Tony Grove--open	9/10/69	1	52	47.3
		2	50	
		3	40	
Tony Grove--under aspen	9/11/69	1	36	37.3
		2	32	
		3	44	
Franklin Basin--under aspen	9/10/69	1	68	65.3
		2	56	
		3	72	
Franklin Basin--under aspen	9/11/69	1	76	72.0
		2	80	
		3	60	

Germination under 25 C (8 hours)-15 C (16 hours) of temperature and 8 hours photoperiod

Table 22. Results of germination of seeds collected from one plant of Rudbeckia occidentalis at different locations within the State of Utah, 1970

Source	Date collection	Replication	Percent germination	Average
Mud Creek (7,200 feet) open	9/9/70	1	88	90.6
		2	88	
		3	96	
Mud Creek (7,200 feet) open	9/9/70	1	84	85.3
		2	80	
		3	92	
Mud Creek--under aspen	10/9/70	1	92	92.0
		2	92	
		3	92	
Mud Creek--under aspen	10/9/70	1	92	92.0
		2	92	
		3	92	
Tony Grove--under aspen	10/10/70	1	72	69.3
		2	68	
		3	68	
Tony Grove--under aspen	10/10/70	1	65	67.6
		2	79	
		3	68	
Tony Grove--open	10/10/70	1	60	60.0
		2	58	
		3	62	
Franklin Basin--under aspen	10/11/70	1	70	68.3
		2	67	
		3	68	
Franklin Basin--under aspen	10/11/70	1	65	65.0
		2	65	
		3	68	

Germination under 25 C(8 hours)-15 C (16 hours) of temperature and 8 hours photoperiod

Table 23. Results of the application of 2, 3, 5-Triphenol-2H-tetrazolium chloride to seed of Rudbeckia occidentalis that failed to germinate under optimum conditions

Source	Date of collection	Date of test	No. seed treated	No. seed shown color	No. of empty seed
Ephraim- under aspen (10,400)	8/27/69	12/6/69	100	4	96
Ephraim- open (10,400)	8/27/69	12/6/69	100	0	100
Ephraim- under aspen (8,800)	8/29/69	12/6/69	100	40	60
Ephraim- under aspen (8,800)	8/27/69	12/6/69	100	25	75

the same area but lower altitude (8,800 feet) with a better germination percent: 44.0 and 46.6.

In both 1969 and 1970 seeds from the Mud Creek area were high in germination giving 88 and 92 percent, respectively. Seed collections from Tony Grove area had a low germination percentage in 1969 of 47.3 and 37.3 percent; while in 1970 these percentages showed an increase to 67.6 and 60 percent, possibly a reflection of the better climatic conditions during 1970. Seeds from Franklin Basin showed similar trends during both years studied.

To determine whether the failure of seeds to germinate was due to lack of viability the seeds were stained with 2, 3, 5-Triphenol-2H-tretrazolium chloride using seeds from the Ephraim area collected at two elevations, 8,800 feet and 10,400 feet. All filled seeds from these collections gave a positive tetrazolium reaction. The results also show that seeds from higher elevation failed to fill (Table 23) in contrast with seeds from lower altitudes where the percentage of filled seeds was 40 and 25 percent, a relfection of the environmental conditions after the flowers were pollinated.

Another interesting aspect in the study of seeds is the effect of aging with the result that in some plants germination increases with age, while in others it decreases or shows no change. In order to determine the influence of age on "coneflower" seeds a collection made on August 25, 1969, was tested under optimal conditions on November 16, 1969, and, also, on October 14, 1970, after 1 year. The results show no change in the percent germinability during the 1 year (Table 24).

Table 24. Germination results of seeds collected from *Rudbeckia occidentalis* in the Tony Grove area as influenced by the age of the seed

Source	Date of collection	Replication	Percent germination	Average	Date of germination
Tony Grove composite	8/25/69	1	36	40	11/16/69
		2	36		
		3	48		
	8/25/69	1	48	40	10/14/70
		2	36		
		3	36		

Effect of Small Mammals

Relative gopher population of the two exclosures was determined by counting the current year's mounds within each exclosure. Counts were made on July 16, 1969, and on July 21, 1970. Mound counts were converted to number of gophers per hectare (Table 25) according to the population index established by Richens (1964) from studies on the Cache National Forest, Utah.

An increase in burrowing activity occurred at both exclosures in 1970 compared to 1969. One of the reasons for this increase could be due to soil moisture which was higher in 1970 than in 1969.

Pocket gophers feed on the leaves of *R. occidentalis* in addition to other plants and on several occasions it was possible to see this activity. Injuries to the coneflower roots were frequent. Many of the main roots and crowns had been severed by such burrowing activity. Gopher tunnels are, also, extensive near the soil surface and collapse under foot as one walks over them.

It is certain that pocket gophers affect the growth and composition of coneflower in areas such as Tony Grove where it is one of the dominant forbs. However, the specific effects of feeding and burrowing on plant development and changes in composition need more investigation.

Greenhouse Studies on Growth and Powdery Mildew Attack

At the time of seed set during August and September *R. occidentalis* is heavily attacked by powdery mildew in the field. The disease is caused by the fungus *Erysiphe cichoracearum* DC. ex Merat (Schmitt, 1955a). As is true

Table 25. Mound numbers and estimated pocket gophers (Thomomys talpoides) per hectare at two exclosures in the Tony Grove area

Exclosure	July 16, 1969 Mounds	July 16, 1969 Population	July 21, 1970 Mounds	July 21, 1970 Population
Lower No. 1	1,956	Ca. 80	2,176	Ca. 94
Upper No. 2	1,730	Ca. 76	1,856	Ca. 82

of other members of the family Erysiphaceae this fungus is an obligate parasite and will not grow on non-living tissue. E. cichoracearum has a wide host range which includes members of a number of plant families. Within the species are several physiologic races each of which is host specific and is distinguished from other races only on the basis of host range (Schmitt, 1955b).

Field observation indicated a relationship between leaf growth and mildew development. Examination showed that only those plants in which leaf growth has ceased were these signs of the disease. Younger plants showed less infection or no symptoms at all in the case of new rosettes. Symptoms varied somewhat but usually the mycellia and spores developed extensively on the upper surfaces of the leaves before any symptoms became apparent on the stems. As the disease advanced the fungus spread over the entire plant, including both leaf surfaces, and thereby imparted a dusty gray-green cast to the infected area. Within a period of a few days the diseased plants began to wilt, and within 2 to 4 weeks the plants became brown and died.

Because young leaves of new rosettes showed no symptoms of attack it was believed that the disease affects the leaves of the plants when growth has ceased. At this time they are more susceptible to infection than when the leaves are growing. So, by application of gibberellic acid (GA_3) solution as a leaf spray to promote regrowth after clipping 100 percent of the plants, the above assumption was tested.

The results (Table 26) show that with the application of 100 ppm per plant of GA_3 leaves were stimulated to fast growth, especially the petioles. However, growth also ceased first in comparison with the check plants, where growth continued for an additional 2 weeks. During the growth period for both treatments no mildew attack was observed--the first 2 weeks. Thereafter, symptoms of mildew attack were detected increasingly in the GA_3 treatments to complete infection. At the end of the experiment, the GA_3 treatment showed an average attack of 7.12 (in a scale from 0 to 10), while the check plants showed only 2.0.

The other two treatments of GA_3 applications (200 ppm and 300 ppm in two and three applications, respectively) showed during the first 2 weeks trends similar to the 100 ppm application. After that an abnormal growth was apparent, with the leaves completely distorted and with less infection of mildew, which at the end of the experiment was slightly higher than in the check plants. The averages were 3.7 for 200 ppm GA_3 application and 2.25 for 300 ppm application.

From these results it is apparent that when the leaves have ceased growth they are most susceptible to mildew attacks (vigor of growth). However, some mildew symptoms may appear even if the leaves are growing.

Table 26. Characteristics of the leaves and mildew attack after application of gibberelic acid to *Rubdeckia occidentalis* plants

		7/29/70			8/5/70			8/12/70			8/19/70	
Treatment	Replication	Leaf length	Petiole length	Mildew attack	Leaf length	Petiole length	Mildew attack	Leaf length	Petiole length	Mildew attack	Observations	Mildew attack
100 ppm GA	1	5.1	2.2	0	11	2.2	1	11	2.2	4	Normal growth	7
	2	4.7	2.4	0	11	2.5	1	11	2.5	4		6.5
	3	4.8	1.9	0	9	1.9	1	9	1.9	4		8
	4	5.2	2.5	0	12	2.4	1	12	2.4	4		7
	Average	4.95	2.25	0	10.7	2.25	1	10.7	2.25	4		7.12
200 ppm GA	1	4.7	2.3	0	9	2.5	1	7.0	2.6	3.0	Abnormal growth	4.0
	2	4.8	2.2	0	8	2.4	1	6.5	2.6	3.5	Leaves distorted	3.5
	3	4.7	2.3	0	15	2.6	1	14.0	2.8	2.5		3.0
	4	5.2	2.2	0	16	2.3	1	15.1	2.5	3.0		3.5
	Average	4.85	2.25	0	12.0	2.45	1	10.82	2.62	3.0		3.7
300 ppm GA	1	5.1	2.4	0	12	2.8	0	10.2	2.7	1.0	Very adnormal growth	2.0
	2	5.2	2.1	0	12	2.5	0	6.3	3.1	1.0	Leaves distorted	2.0
	3	4.5	2.4	0	13	2.6	0	9.2	3.0	1.0		2.5
	4	4.7	2.1	0	9	2.4	0	8.0	2.8	1.0		2.5
	Average	4.82	2.22	0	11.5	2.56	0	8.67	2.9	1.0		2.25
Check	1	4.0	1.8	0	11	2.5	0	11.0	2.5	1.0	Normal growth	2.0
	2	3.8	1.7	0	11	2.1	0	11.5	2.0	0.5		2.0
	3	4.5	1.5	0	10	2.0	0	11.0	2.0	0.5		2.0
	4	4.2	2.2	0	9	2.5	0	10.8	2.6	0.5		2.0
	Average	4.12	1.8	0	10.2	2.22	0	11.07	2.22	0.62		2.0

Field observations showed that some coneflower plants went without bolting or flowering throughout the growing season and yet showed vigorous growth. Some kind of fertilization (for example, by livestock manure) may be responsible for this phenomenon, especially the effect of nitrogen.

Tisdale and Werner (1966) said that an adequate supply of nitrogen is associated with vigorous vegetative growth and a deep green color. Excessive quantities of nitrogen can, under some conditions, prolong the growing period and delay maturity. This is most likely to occur when adequately supplied water and other plant nutrients are present.

Applications of an equivalent of 40 kgs/Ha of ammonium sulfate (21 percent) were made to plants of R. occidentalis growing in the greenhouse in soil from the Tony Grove area. In general, nitrogen application maintained the plants in the rosette stage, while plants without nitrogen during the same period of observation, from January 4 to March 1, 1970, went from rosette to bolting and ultimately to flowering.

Upon analyzing the influence of nitrogen on the morphology of the plants leaf width was significantly greater on plants with nitrogen than on check plants. The averages were 11.3 versus 5.3 cm, respectively. The same results were attained for leaf length--15.3 cm for plants with nitrogen and 9.3 cm for the check plants (Figure 13).

Speculation on the application of these results to field conditions leads to a conclusion that when some plants are supplied with nitrogen (livestock manure) vegetative growth in the rosette stage is prolonged. Then when plants

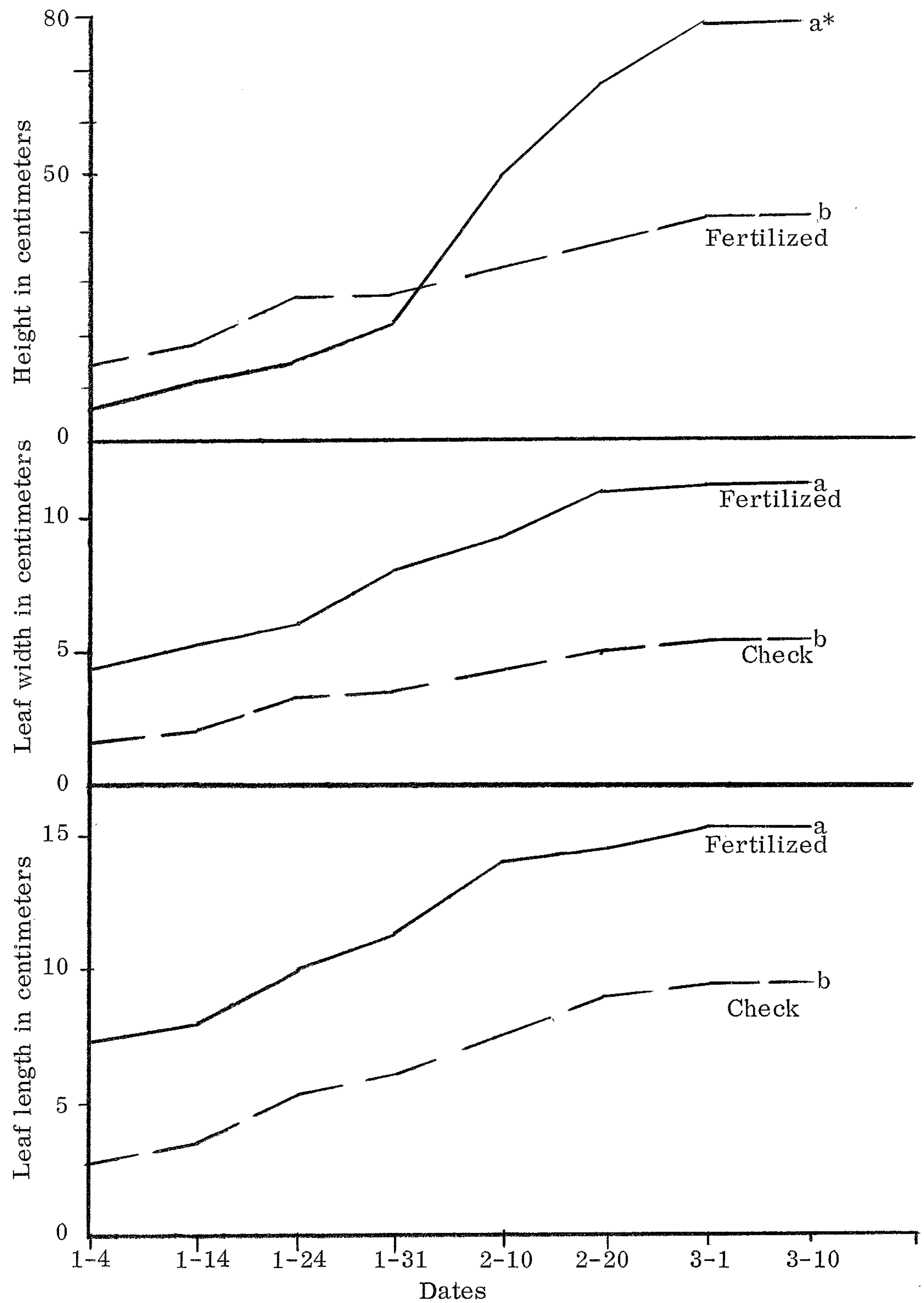


Figure 13. Effect of nitrogen application upon the height and leaf development in Rudbeckia occidentalis.*

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

are ready to go to the next stage, adverse environmental conditions such as low temperature or short photoperiod may be inhibitory so that the plants remain in the rosette stage until the next season.

Plants with and without nitrogen application were placed in the growth chamber environment with alternating temperatures of 25-15 C and 18 hours of light to confirm the results found under greenhouse conditions. Plants without nitrogen application bolted and flowered. Fertilized plants remained in the rosette stage.

Dormancy and Photoperiodic Studies

Flowering in Rudbeckia occidentalis is not the result of a series of independent processes determined solely by the genetic constitution but is controlled by environmental factors which interact with the genetic constitution in a specific manner. The two climatic factors which play by far the most important role in controlling flower development are temperature and day length. However, with available facilities it was only possible to study the effect of photoperiod (long and short day length) on the growth and development of R. occidentalis under growth chamber conditions with alternating temperatures of 25 C-15 C (16 hours-8 hours).

R. occidentalis is primarily a long-day plant. This conclusion was reached from a study where one set of plants composed of three plants without cold treatment and eight plants with cold treatment were under 12 hours of photoperiod and another similar set under 18 hours photoperiod. As shown in

Table 27 and Figure 14, only those plants under long-day photoperiod (18 hours) flowered while those under 12 hours of light remained in the rosette stage during all of the period of observation (1/31/70 to 3/21/70). Plants with and without cold treatment flowered under a long day photoperiod indicating that cold treatment is not required for the flowering process.

Vegetative development was rapid for plants under an 18-hour photoperiod. In a period of 2 weeks plants that were in the rosette stage began to bolt and ultimately flowered. Conversely those plants under 12 hours of light remained in the rosette stage and growth occurred only in the leaves which elongated to produce a vigorous rosetts (Figure 15). However, the height reached by plants under 18 hours light was mainly due to the growth of the stems. In the other treatment (12 hours light) the height was due to the length of leaves, while the undeveloped stems are unelongated and hidden in the middle of the rosettes. The height attained by the plants at the end of the trial under 18 hours light averaged 62.6 cm for those with a cold treatment and 55.0 cm for those without a cold treatment. These results were statistically significant at the 5 percent level. In this analysis plants No. 1, 2, and 3 were used as replications for 12 hour light, and plants No. 4, 5, and 6 were replications for the 18 hour light treatment. The heights of the plants under 12 hours light averaged 17.2 cm for those with cold treatment, and 6.8 cm for those without cold treatment. Comparing cold treatment versus no cold treatments, no statistically significant results were obtained by varying the photoperiod from 12 to 18 hours.

Table 27. Phenological development of Rudbeckia occidentalis plants under some alternate temperatures (25 C-15 C) but different photoperiods

	Treatment of light																					
	12 hours											18 hours										
	Plant number											Plant number										
	1	2	3	4	5	6	7	8	9	10	11	1	2	3	4	5	6	7	8	9	10	11
Date	No cold treatment			With cold treatment								No cold treatment			With cold treatment							
1/31/70	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
2/4/70	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
2/8/70	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
2/14/70	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	B	R	R
2/19/70	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	B	R	R
2/23/70	R	R	R	R	R	R	R	R	R	R	R	R	B	R	R	R	R	R	R	B	R	R
2/26/70	R	R	R	R	R	R	R	R	R	R	R	B	B	R	R	R	R	B	R	B	R	R
3/3/70	R	R	R	R	R	R	R	R	R	R	R	B	B	R	B	R	R	B	R	B	B	R
3/8/70	R	R	R	R	R	R	R	R	R	R	R	B	B	R	B	R	R	B	R	B	B	R
3/14/70	R	R	R	R	R	R	R	R	R	R	R	B	B	R	B	B	R	B	R	B	B	R
3/21/70	R	R	R	R	R	R	R	R	R	R	R	F	B	R	B	B	R	F	R	F	B	R

R = Rosette
B = Bolting
F = Flowering

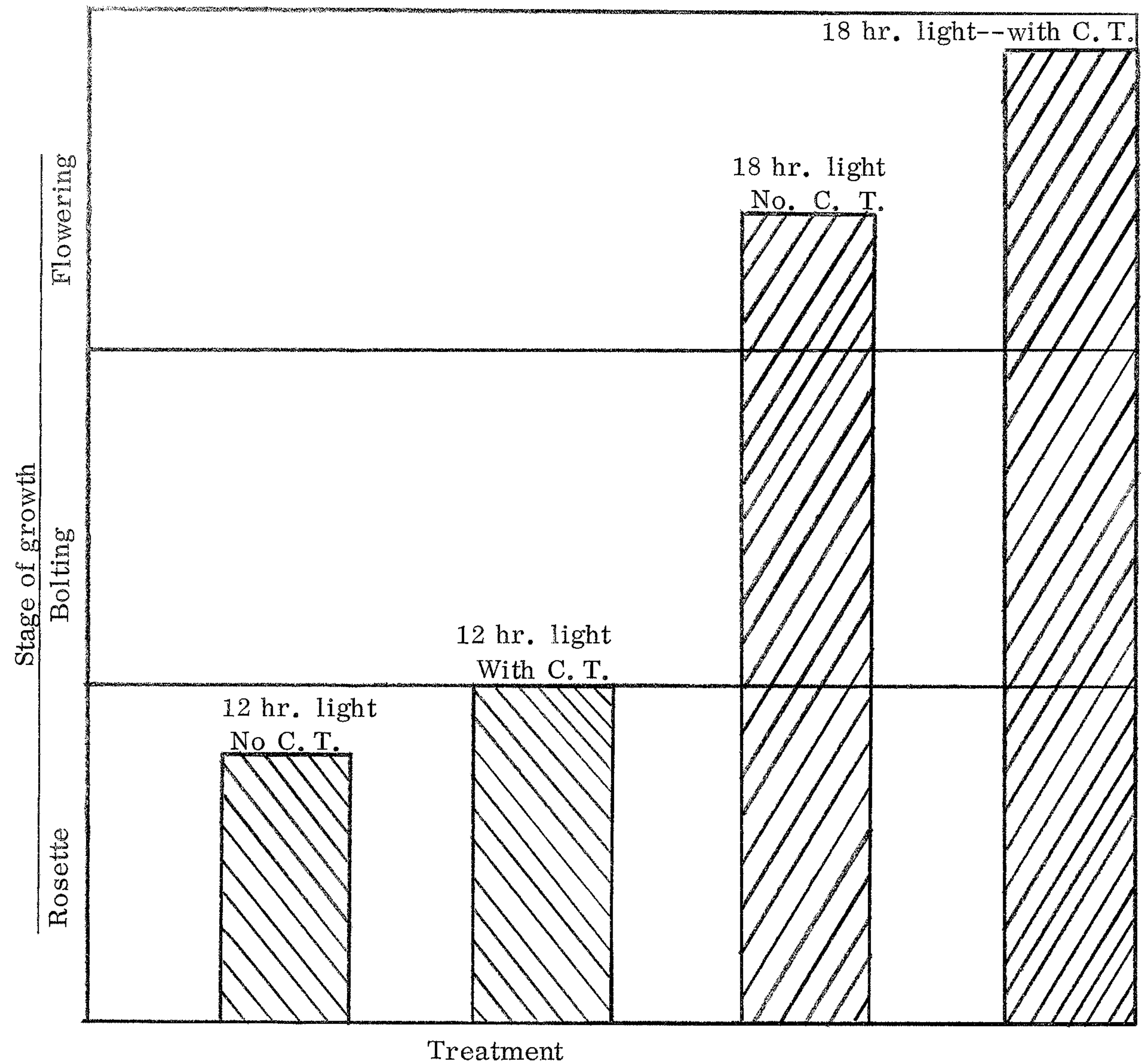


Figure 14. Stage of growth attained by Rudbeckia occidentalis plants, under same alternate temperature (25 C-15 C) but different photoperiod and cold treatment.

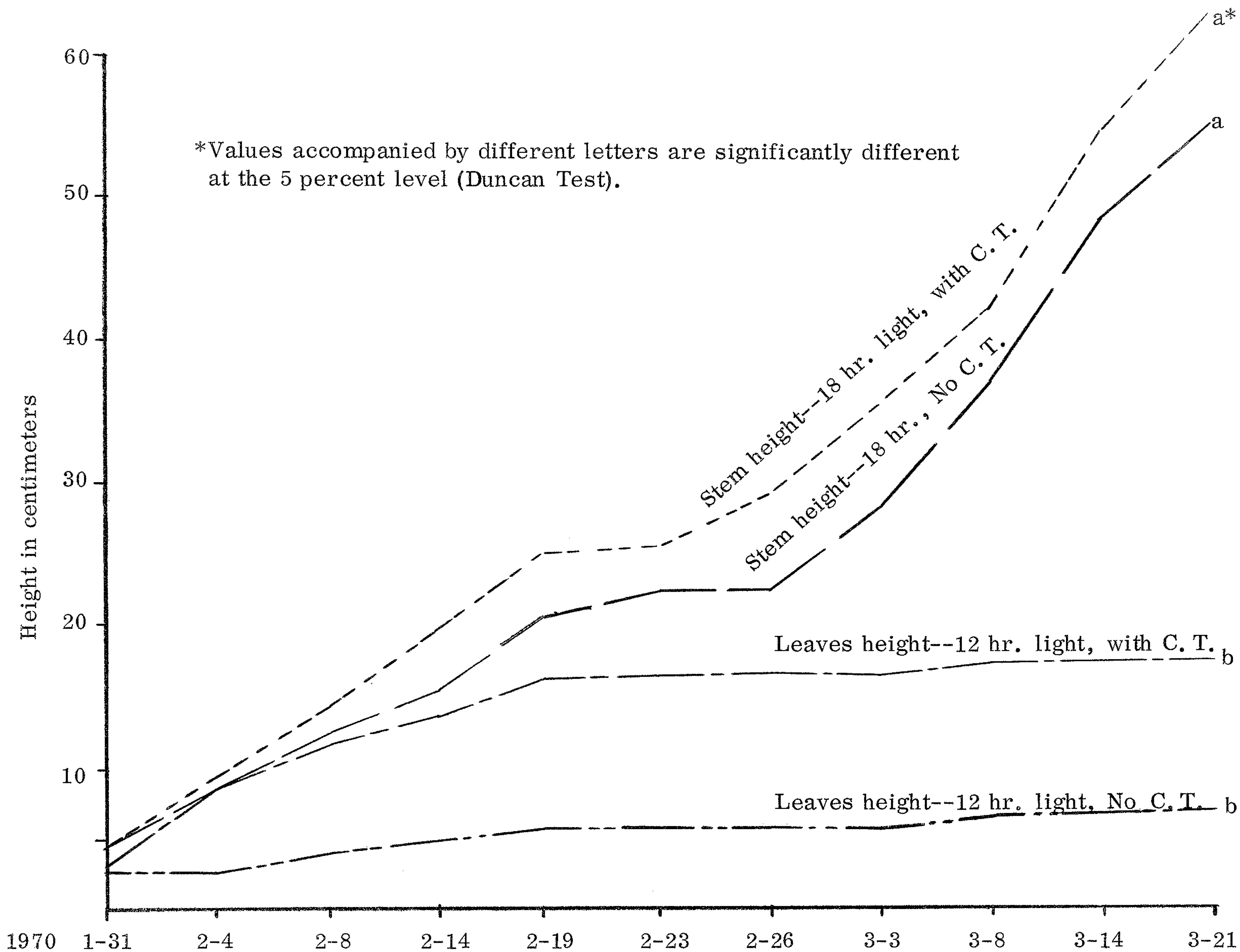


Figure 15. Growth and development measured in terms of height (in centimeters) attained by Rudbeckia occidentalis plants under same alternate temperature (25 C-15C) but different photoperiod and cold treatment (C. T.).

Heights attained by plants under both light treatments appear to be mainly a function of the life cycle stage developed under the influence of photoperiod. Comparisons as discussed above in terms of height (using rosette for the 12 hour light versus bolting and flowering for the 18 hour light) are apparently not good indicators of the influence of photoperiod over the vegetative development of the studied plant. Leaf growth under both situations may give a better idea.

Figure 16 shows the growth sequence of leaves (in length of the lamina) during the study period. At the end of the trial there was not a statistically significant difference between leaf length of plants with and without cold treatment under 18 hour light. However, both treatments are statistically significant for leaf length of plants with and without cold treatments under 12 hour light. Leaf length of plants with cold treatment under 12 hour light were statistically significant over leaf length of plants without cold treatment.

Similar results are shown in Figure 17 relating to the leaf width of the lamina under the same treatments. However, here there are no statistically significant differences over the treatments with and without cold treatment under 18 hour light and with cold treatment under 12 hour light. A generalization from the above results is that with long photoperiod (18 hour light) there are no significant differences in the leaf area of plants subjected to cold treatment and plants without it. On the other hand, under the short photoperiod (12 hours) when Rudbeckia plants remain in the rosette

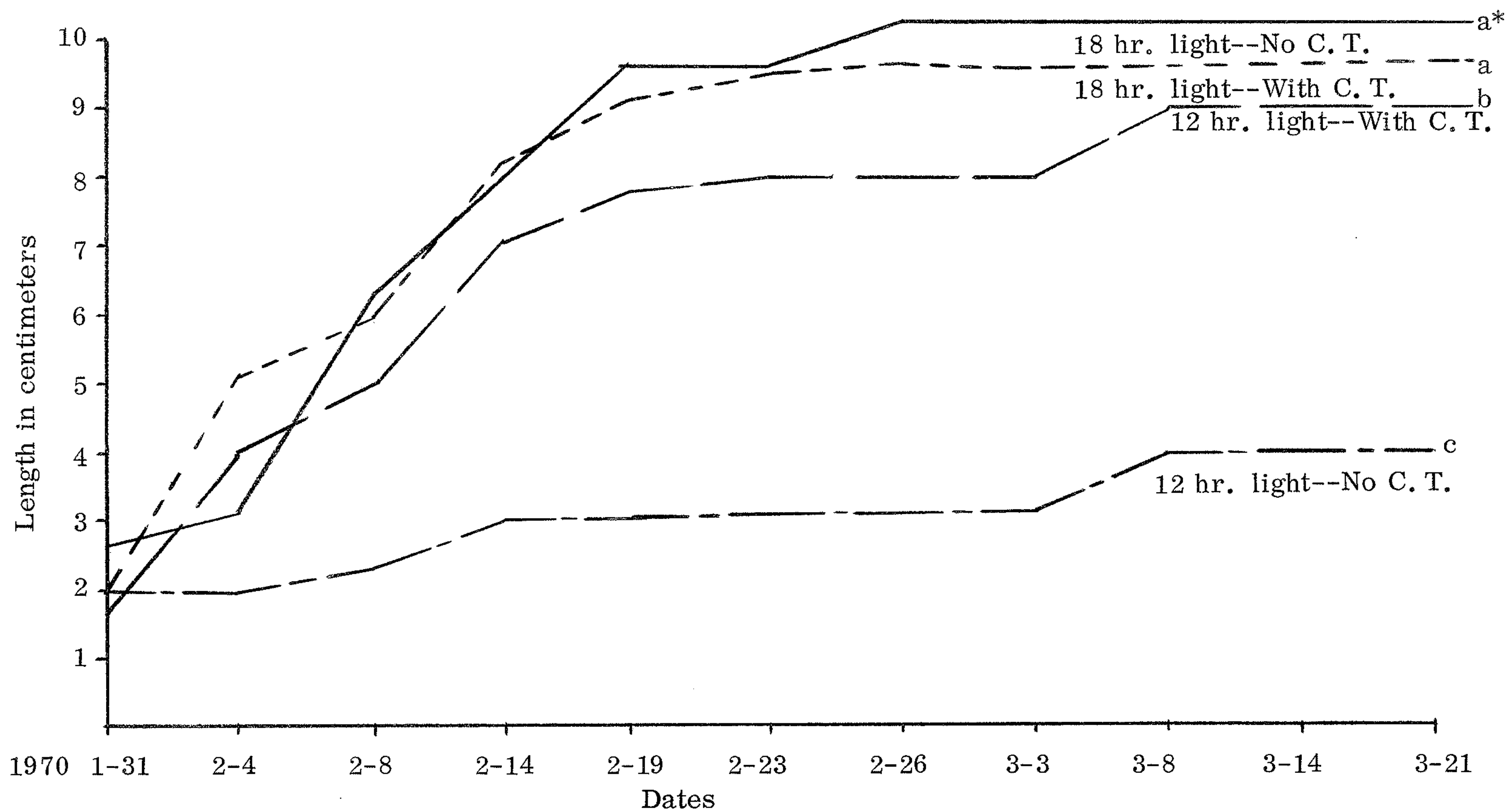


Figure 16. Average leaf length growth of <u>Rudbeckia occidentalis</u> plants under same alternate temperatures (25 C-15 C) but different photoperiod and cold treatment.

---

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

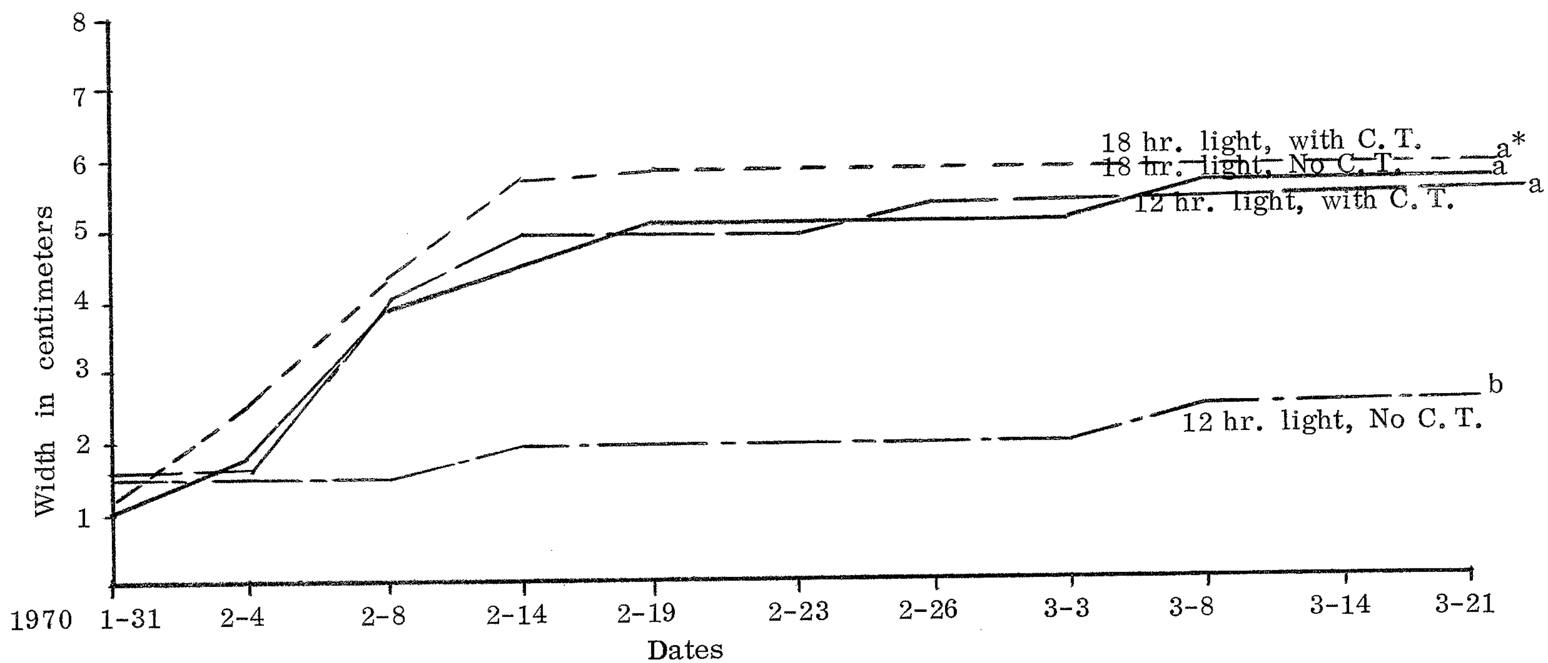


Figure 17. Average leaf width growth of Rudbeckia occidentalis plants under same alternate temperature (25 C-15 C) but different photoperiod and cold treatment.

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

stage, cold treatment has an interesting effect in the leaf area development. Leaves without cold treatment are significantly smaller than leaves with cold treatments.

As Salisbury and Ross (1969) indicated, an important positive response of plants to low temperature is the effect of low temperature upon the vegetative form and growth of certain plants. We are concerned mostly with inductive (delayed) effects upon some developmental plant process. Such effects may also be observed in response to the length of the day and perhaps to other environmental factor as well. In fact, low temperature and day length effects are frequently interrelated but the physiological mechanisms are difficult to explain at the moment. Further work might explain why leaves without cold treatment are smaller than leaves with cold treatment under short photoperiod. It is also interesting to refer, at this point, to the remarks of Steward (1968) that environmental factors that are known to determine morphogenesis also affect metabolic patterns. It is difficult to separate the metabolic cause of morphogenetic events from those responses which result from the changed growth when a given morphogenetic stimulus is initiated.

Results were similar under both growth chamber and greenhouse conditions (Table 28). Plants without cold treatment and plants that had varying natural cold treatment in the field from December to March were set on two benches, one with natural greenhouse conditions and short winter photoperiods and the other with additional supplementary fluorescent light for a photoperiod of 16 hours.

Table 28. Phenological development of plants of Rudbeckia occidentalis with and without natural cold treatment under long and short photoperiod in greenhouse conditions from January 5 to April 20, 1970

Plant No.	Treatment	Dates of stage of development				Plant measurements at seed set			Percent germination
		Rosette	Bolting	Flowering	Seed set	Height cm	Leaf width	Leaf length	
A. 16 hours photoperiod									
1	No cold treatment	Jan. 8	Jan. 20	Feb. 5	Feb. 15	98	5.0 cm	9 cm	25
2	No cold treatment	Jan. 8	Jan. 19	Feb. 3	Feb. 13	101	5.0	10	20
3	With C. T.-Dec. 18-69	Jan. 15	Jan. 30	Feb. 20	March 2	80	5.0	9	--
4	With C. T.-Jan. 15-70	Jan. 25	Feb. 10	Feb. 27	March 12	82	5.5	9	17
5	With C. T.-Feb. 19-70	Feb. 28	March 21	April 5	April 18	95	5.0	10	18
B. Normal greenhouse photoperiod--(short)									
1	No cold treatment	Jan. 8	---	---	---	6.5	2.5	4.0	--
2	No cold treatment	Jan. 7	---	---	---	6.0	2.5	4.0	--
3	With C. T.-Dec. 18-69	Jan. 15	---	---	---	8.0	3.0	6.0	--
4	With C. T.-Dec. 15-70	Jan. 23	---	---	---	8.5	3.0	6.0	--
5	With C. T. Feb. 19-70	Feb. 27	---	---	---	8.0	3.0	5.5	--

Plants under long photoperiod, regardless of the cold treatment, bolted, flowered and set seed. Seeds for germination studies were obtained from all the plants except plant No. 3, which suffered a heavy attack of mildew. There were no differences in leaf area between the plants with and without cold treatments. Plants with cold treatment which were collected each month from December to February from the field attained their normal stages of growth at regular intervals.

Plants under natural greenhouse conditions (short winter photoperiod) remained in the rosette stage regardless of cold treatment. However, the leaf area in the plants with no cold treatment was smaller than the leaf area of plants with cold treatments.

Competition and Flowering in Young Plants

Plants show extreme plasticity as they respond remarkably in size and form to environmental conditions. One of the most potent of these external forces is the presence of competing neighbors which may reduce a plant to a diminutive size. The contrast between the growth of an isolated plant and that of a plant growing under competitive stress is shown in Figure 18, which compares stages of growth attained in the second year. When plants were widely spaced (20 x 20 cm) under favorable conditions of water, light and nutrient supply so that no competition occurs between them, they continued to grow to a nearly constant rate until they passed from the vegetative rosette stage to bolting, flowering and finally to seed production. In contrast, plants which

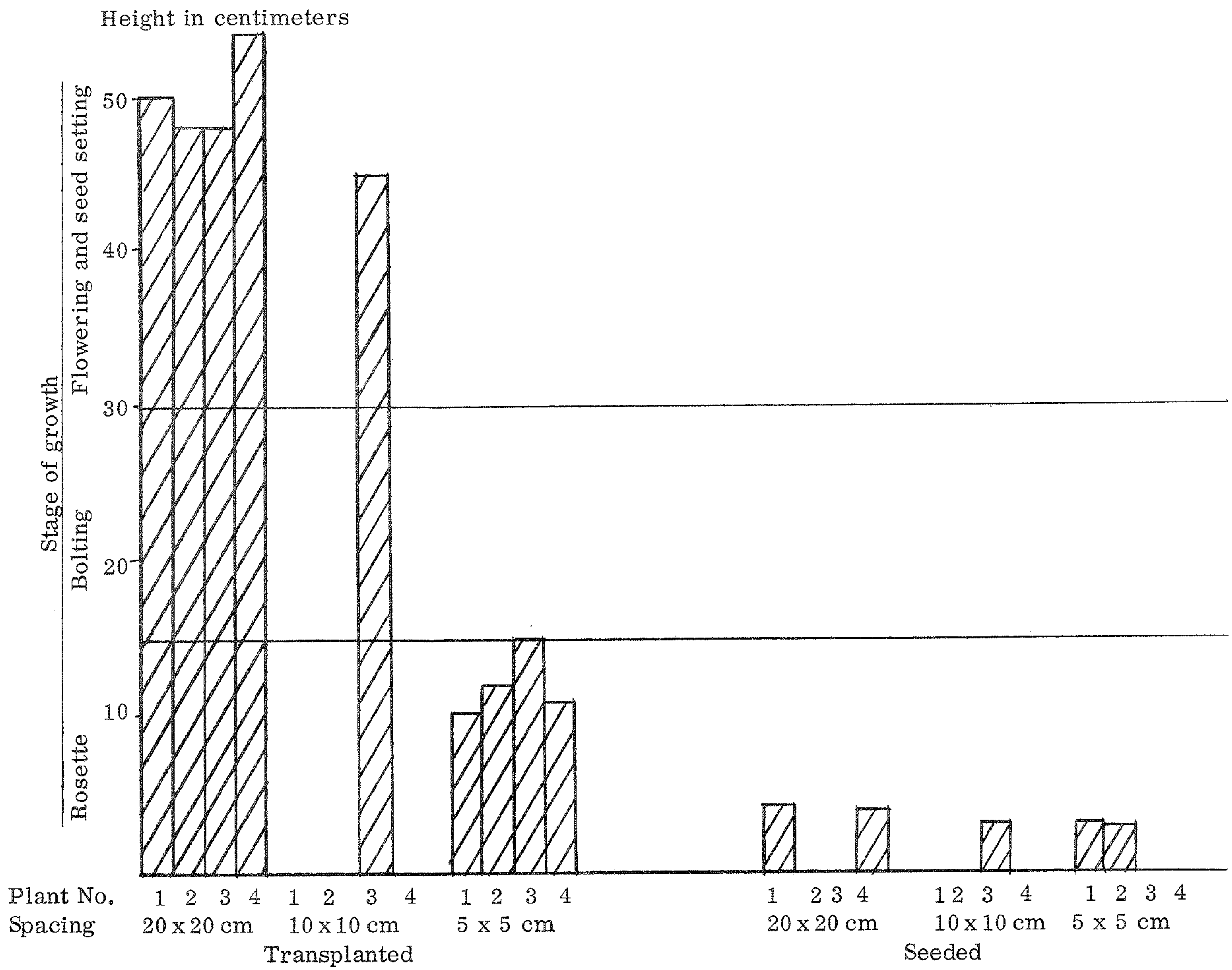


Figure 18. Stage of growth and height attained by 2 year old seedlings of Rudbeckia occidentalis transplanted and seeded under different spacing treatments.

entered into early competition (5 x 5 spacing) with their neighbors immediately showed a reduction in growth which became progressively marked as competition intensified so that the plants remained in the vegetative stage.

Competition for light differs from that for nutrients, water or carbon dioxide in that there is no common pool from which plants continue to draw their supply until it is depleted or exhausted. Light energy is instantaneously available and it must be immediately intercepted or it will be lost as a source of energy for photosynthesis.

It follows that the successful plant is not necessarily the plant with more foliage, but the plant which has its foliage in an advantageous position relative to the foliage of its competitors for light interception.

In the case of 2 year old Rudbeckia apparently the process of competition for light is not immediately one of competition among plants. It is competition among leaves. If one leaf lies above another, as was the case in the 5 x 5 cm spacing, then the depression of the photosynthetic rate of the lower leaf will be the same, whether the superior leaf is of the same plant or another. This competition between leaves was especially evident in the dense treatment at 5 x 5 cm and partially evident in the 10 x 10 cm spacing. So, there is a difference in development of plants widely spaced which flowered, in contrast with those in a high density planting which remained vegetative.

During the first year of the competition studies (Table 29) no signs of competition were observed among the spacing treatments. The major differences were in the vigor and percentage survival of seedlings 2 weeks old that had been germinated in petri dishes in the laboratory and started in the

Table 29. Chronological development of *Rudbeckia occidentalis* plantings for competition studies during the first year, 1969

Seedlings

Date of transplanting: June 23, 1969

Stage attained before snow cover (December, 1969): rosette

Average height of seedlings: 3 cm

Differences among spacing treatments: No differences

Survival before snow cover: 100 percent

Seeds

Date of seeding: June 24, 1969

Date of first seedling emerged: August 6, 1969

Date of 100 percent of seedling emerged: August 15, 1969

Stage attained before snow cover (December, 1969): rosette

Average height of seedlings: 1.2 cm

Differences among spacing treatment: No differences

Survival before snow cover: 40 percent

greenhouse, compared to similar treatments using seeds directly seeded in the field. Before the snow cover developed (December, 1969) survival from transplanting was 100 percent, while in the seeded treatments it was 40 percent. Also, the average height attained by the transplanted seedlings was 3 cm, while the seedling germinated in the field reached an average height of only 1.2 cm.

During the second year (1970) all transplanted seedlings in the 20 x 20 cm spacing produced flowers. One out of four seedlings flowered in the 10 x 10 cm spacing treatment. All the other seedlings (5 x 5 cm spacing) and the survivors from the seeded plants, even at the spacing of 20 x 20 cm, remained vegetative. Here is seen a different response to transplanting versus direct seedling in the field. Apparently, as shown in Table 20, Rudbeckia seeds germinate better if light is supplied at optimum temperature and water conditions. Similar results were obtained by Mitchel (1926) who germinated seeds of R. hirta at 20 to 25 C in diffuse light or darkness. In light, germination was 56 percent in 5 days and in darkness, 52 percent in 12 days.

Those seedlings (2 weeks old) that were germinated under optimum conditions in the growth chamber were able to cope better with the environmental conditions when transplanted to the field than the seedling that emerged from seeds planted directly in the field.

Climatological data for the study area (Table 30) explain why the rosette stage was attained on May 6 (Figure 18), in contrast with the Tony Grove area, where this stage was attained on May 29 for 1969 and July 11

Table 30. Climatological data at Utah State University, Logan, from January to August of 1970

Month	Temperature: Average maximum	Average minimum	Average	Lowest	Date	Total percent
January	36.3	22.8	29.6	-4	8	4.1
February	45.4	27.8	36.6	16	19	2.5
March	46.0	26.8	36.4	17	20	5.8
April	49.8	30.8	40.3	18	1	9.7
May	65.8	43.4	54.6	30	1	.0
June	77.4	53.7	65.6	43	30	.0
July						
August	88.3	60.8	74.6	52	9	.0

for 1970 (Table 14), an advance of 3 weeks. The logical explanation is in temperature differences which are optimum for regrowth at an early data (May 6) at the Utah State University Weather Station, while at much higher altitude at Tony Grove, optimum temperatures are reached by the end of May or the beginning of June.

Inhibitor Studies

Since Carnahan and Hull (1962) reported inhibitory effect of Rudbeckia occidentalis on intermediate wheatgrass and radish, several studies were undertaken here to determine whether there were specific inhibitory substances in Rudbeckia and whether these substances prevented or reduced germination of associated species.

Since various concentrations of Rudbeckia leachate may occur in field soils, it was important to have a standard concentration as a basis for all experiments and to determine with dilutions, if any, inhibit the germination of seeds or the growth of seedlings. On January 6, 1970, a standard leachate was obtained by blending 5 grams of air-dry Rudbeckia leaves in 100 ml of distilled water and holding the resulting slurry for 24 hours at room temperature before filtration. Various dilutions of the filtrate (leachate) were then tested for inhibitory effects.

The experiment was begun on January 8, 1970. A five-treatment leachate concentration design (three replications) with two grass species in each treatment was used. Manchar smooth brome and Nordan crested wheatgrass were used as the test species. Germination in these species began on January 18. Counts were made each day until January 24, 1970. The check treatment (4 ml of distilled water) gave a highly significant higher germination percentage compared with the leachate concentration treatments (Table 31). In both grass species full strength leachate gave a significantly lower germination percentage than any other treatment.

There was a general trend for the higher concentrations of leachate to increase the inhibitory effects upon seed germination. Leachate concentrations produced abnormal growth in the seedlings, especially in root development.

Table 31. Percent germination of seeds of Manchar Brome grass and Nordan wheatgrass when different concentrations of Rudbeckia leachate were used in the germination medium

Treatment	Manchar Brome % germination	Nordan wheatgrass % germination
1. 1 ml leachate + 3 ml water	62.4b*	56.0b
2. 2 ml leachate + 2 ml water	41.2bc	6.00b
3. 3 ml leachate + 1 ml water	45.2bc	36.0c
4. 4 ml leachate	38.4c	37.2c
5. 4 ml distilled water	85.2a	77.2a

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

In coleoptile development there was a general trend toward inhibition as the concentration of leachate increased (Table 32), especially at the higher concentrations. Low concentrations (for example, 1 ml of leachate for Manchar Brome and 1 ml and 2 ml of leachate for Nordan wheatgrass) apparently do not affect coleoptile development significantly.

Root development showed the most significant response to the leachate concentration. In both grass species, from the check (distilled water) through the low to higher concentration of leachate, significant reductions in root length were obtained (Figure 19).

The previous experiment showed that the inhibitory substance are readily soluble in water. In an attempt to isolate specific inhibitory substances from coneflower plant material, several preliminary studies were undertaken.

Table 32. Coleoptile and root growth of seedlings of Manchar brome grass and Nordan wheatgrass when different concentrations of Rudbeckia leachate were used in the germination medium

Treatment	Manchar brome		Nordan wheatgrass	
	Coleoptile	Root	Coleptile	Root
1. 1 ml leachate + 3 ml water	6.5 cm a b	2.5 cm b	6.8 cm a	5.6 cm b
2. 2 ml leachate + 2 ml water	6.0 b	2.2 c	7.0 a	4.3 c
3. 3 ml leachate + 1 ml water	5.3 c	0.7 d	5.3 b	1.3 d
4. 4 ml leachate	3.8 d	0.3 e	3.6 c	0.4 e
5. 4 ml water	7.0 a	2.7 a	7.3 a	8.3 a

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

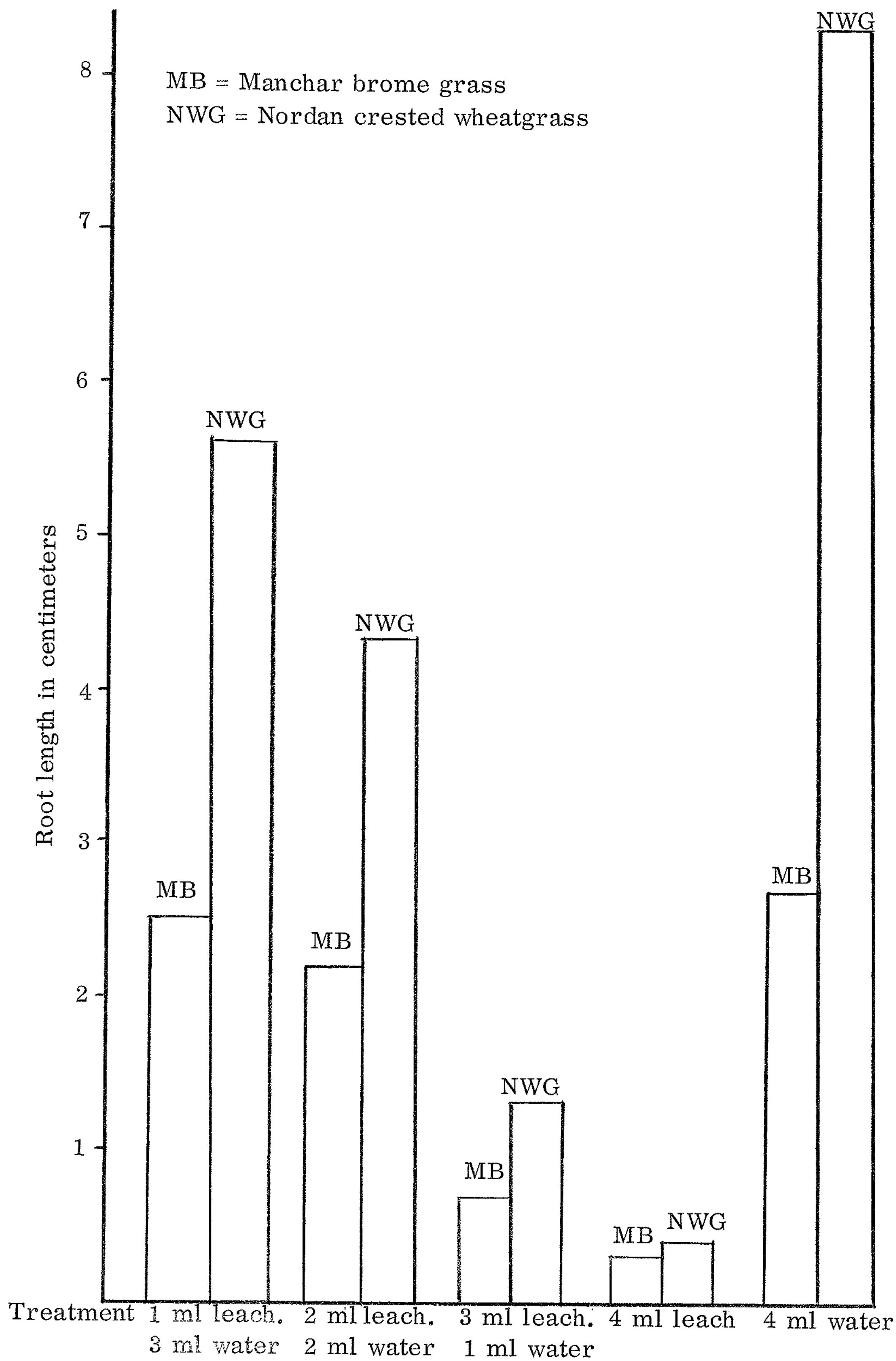


Figure 19. Root development of Manchar brome grass and Nordan wheatgrass when different concentrations of Rudbeckia leachate was used in the germination medium.

Leachate from coneflower plants was boiled for 5 minutes and then the solution was tested on seeds of Nordan wheatgrass. The results showed that the inhibitory substance was not destroyed or inactivated, but rather appeared to be more active than the unboiled leachate.

In another study on the effects of the leachate, activated charcoal (Norit A) was added to the leachate and the suspension was filtered and centrifuged before use. The results showed the same inhibitory activity on the germination of the wheatgrass seeds and also on root development. However, coleptile growth was nearly normal.

Leachate of coneflower was placed in dialysis tubing and dialyzed against distilled water for 24 hours. A high concentration of inhibitory substances appeared to have moved out through the dialysis tubing into the distilled water because the inhibitory effect of the original leachate on root growth was removed. The leachate remaining in the dialysis tubing did not appear to be as inhibitory as the undialyzed leachate. As proteins and other high molecular weight organic compounds molecules are too large to move through the dialysis tubing, these compouds can be ruled out as being the inhibitory substances.

Leachate kept in a refrigerator for several days showed a similar inhibitory effect on germination and root development of Nordan wheatgrass seeds (Figure 20).

Chromatography studies using coneflower extract with distilled water buthanol and 40 percent methanol as developing solvents gave similar results,

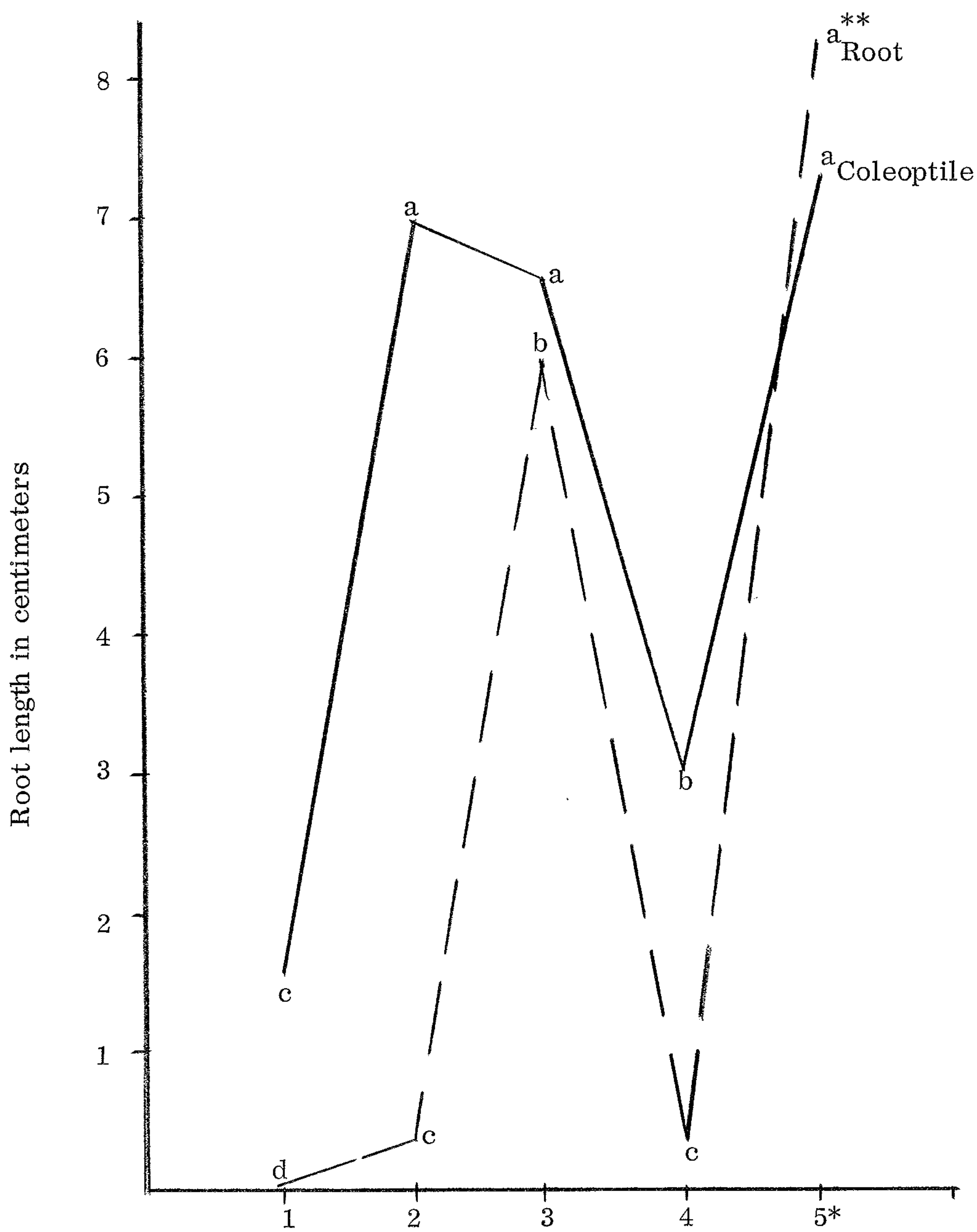


Figure 20. Coleoptile and root development of seedlings of Nordan wheatgrass germinated in leachate of Rudbeckia occidentalis, subjected to different treatments.

*Treatments: 1. 15 ml of extract, boil and simmer; 2. 15 ml of extract plus 1 gm of activated charcoal (Norit A) for 24 hours: Filger and centrifugated 5 minutes; 3. 15 ml of extract, dialyzed in distilled water for 24 hours; 4. Extract keep water refrigerated; 5. Check, seed germinated under distilled water.

**a, b, c, d means statistically significant by the Multiple Duncan's Test at the 5 percent level.

except that a trace buthanol which remained in the paper after air-drying apparently was inhibitory to the development of Nordan wheatgrass seeds.

Distilled water as a solvent caused coneflower leachate to rise on the chromatographic paper to a maximum height of 25.5 cm after 24 hours. The paper was divided into five equal segments of 5.1 cm each. These segments were tested for inhibitory activity using seeds of Nordan wheatgrass. Sufficient distilled water was added to the individual segments in petri dishes to insure germination of uninhibited seeds. Buthanol solvent allowed the leachate to rise on the chromatographic paper to a height of 11 cm and methanol to 21 cm. Both papers were then divided into five equal segments and tested in the same way as with distilled water as the solvent. Both distilled water and methanol showed that the segment which inhibited root growth was in the RF range of 0.8-1.0 in both cases, as shown in Table 33.

To see if inhibition also applied to coneflower, seeds of coneflower were tested in coneflower leachate. Similar trials as discussed above were done, also, with extract of tomato leaves and mountain brome.

When coneflower seeds were tested in their own leachate, the results showed significant inhibition in germination for the treatment with 2 ml leachate + 2 ml distilled water, an average of 21.3 percent compared to the check treatment (29.3 percent). However, if we compare hypocotyl and root growth leachate, as a germination medium, significantly inhibited hypocotyl growth but not root growth, as was the case with the other experiments discussed above (Table 34).

Table 33. Percent germination, coleoptile and root growth of Nordan wheatgrass when chromatography paper is put under different developing solvents for the Rudbeckia occidentalis; leachates were used as a germination medium

Solvent	R. F.	Percent germination	Average growth in centimeters: Coleoptile	Average growth in centimeters: Root
Distilled water	0. -0.2	28	4.1 a *	3.6 a
	0.2-0.4	32	4.0 a	3.3 a
	0.4-0.6	32	4.6 a	3.6 a
	0.6-0.8	32	3.9 a	3.5 a
	0.8-1.0	28	2.4 b	0.5 b
Methanol	0 -0.2	32	4.8 a	1.8 b
	0.2-0.4	24	4.9 a	2.1 a
	0.4-0.6	32	2.4	1.6 b
	0.6-0.8	36	3.1 b	1.2 c
	0.8-1.0	36	1.4 d	0.2 d
Buthanol	0 -0.2	16	No development	
	0.2-0.4	8	No development	
	0.4-0.6	12	No development	
	0.6-0.8	12	No development	
	0.8-1.0	4	No development	

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

Table 34. Percent germination, hypocotyl and root growth of Rudbeckia occidentalis seeds when two concentrations of Rudbeckia leachate were used in the germination medium

Treatment	Replication	Percent germination	Coleoptile	Root
2 ml leachate + 2 ml water	1	20	3.1 cm	2.8
	2	24	3.0	3.0
	3	20	2.8	3.2
	Average	21.3b*	2.7b	3.0a
Check--4 ml of water	1	28	3.3	2.7
	2	28	3.1	3.4
	3	32	2.8	3.2
	Average	29.3a	3.0a	3.1a

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

The effect of tomato leaf extract in different concentrations upon the germination of Nordan wheatgrass gave results similar to those obtained with coneflower leachate. Four ml of leachate from tomato leaves significantly inhibited germination of the tested seeds. Coleoptile and root growth were also significantly inhibited with root development showing the most dramatic response.

Mountain bromegrass is an associated species of R. occidentalis in the study area, and no reports of inhibitors in this particular species were found. Therefore, extracts of mountain bromegrass were also used to determine the effect upon the germination of Nordan wheatgrass (Table 35). Comparing to check treatment with distilled water, the other treatments show progressive inhibition in the percent germination and coleptile and root growth. As the concentration of the germination medium increased by the addition of leachate. The most dramatic response here was in root development which was suppressed at higher concentrations of the leachate.

Apparently, from the results discussed above, the reduction in germination and especially in root development is not due to the presence of specific inhibitors in the leachates used, but to other mechanism such as osmotic effects or enhanced microbial activity. Alternatively, the leachates from a broad range of plants may be shown to contain growth inhibitory compounds when used in sufficiently high concentration under laboratory conditions. These results cast some doubt on the validity of other published reports regarding the significance of specific allelopathic agents.

In order to determine if R. occidentalis produces inhibitors in the field which limits the growth of associated species, mountain bromegrass (the principal associated species) was chosen as an indicator of such inhibitors. Plants of mountain bromegrass were studied with regard to stem height, root length and shoot/root weight ratios in areas where it grew alone and in areas in which it grew associated with Senecio serra or Rudbeckia occidentalis.

The average number of stems per plant of brome growing alone is significantly higher than when growing with Rudbeckia or Senecio (Table 36).

Table 35. Percent germination, coleoptile and root growth of Nordan wheatgrass when different concentrations of Mountain brome grass leachate were used as a germination medium

Treatment	Replication	Percent germination	Average measurement in cm Coleoptile	Root
4 ml water	1	76	8 cm	7 cm
	2	80	9	9
	3	80	8	8
	Average	78.6 a*	8.3 cm a	8.0 cm a
1 ml leachate + 3 ml water	1	72	8	7
	2	68	8	6
	3	64	7	3
	Average	68.0 b	7.6 cm a b	5.1 cm b
2 ml leachate + 2 ml water	1	60	8	0.6
	2	64	8	0.8
	3	72	9	0.7
	Average	65.3 b	8.3 cm a	0.7 cm c
3 ml leachate + 1 ml water	1	52	7	0.6
	2	52	7	0.6
	3	64	8	0.7
	Average	56.0 c	7.0 cm b	0.6 cm c
4 ml leachate	1	24	3	0
	2	40	5	0
	3	40	4	0
	Average	34.6 d	4.0 cm c	0.0 cm d

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan's Test).

Table 36. Differences in the number of stems of Mountain brome grass as affected by growing in association with Rudbeckia occidentalis with Senecio serra and alone

Replication	Treatment		
	Brca-Sese*	Brca-Ruoc	Brca
1	8	4	10
2	5	7	7
3	6	4	13
4	4	5	10
5	2	3	10
6	5	16	8
7	5	5	10
8	3	3	11
9	3	9	8
10	4	5	8
11	10	5	10
12	6	6	7
13	4	12	3
14	2	6	12
15	8	6	11
16	4	2	10
17	2	5	6
18	4	2	15
19	3	3	6
20	5	2	4
Average	4.65	5.50	8.95
	b**	b	a

*Brca = Bromus carinatus
Sese = Senecio serra
Ruoc = Rudbeckia occidentalis

a, b = Statistic significance by the Duncan's Multiple Range Test (0.05).

**Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

Between these last two treatments there are no significant differences. These results appear to be the effect of competition rather than inhibition by coneflower plants.

Brome growing with coneflower gave significantly higher average stem height than brome growing with Senecio, 102.45 cm and 87.90 cm, respectively (Table 37), but is not significant over brome growing alone, which gave an average of 95.30 cm. Moreover, brome growing alone is not significantly different than brome growing with Senecio. An explanation for these results could be that because the morphology of Rudbeckia and Senecio are different. Brome grows higher with Rudbeckia because of more light competition than with Senecio.

Roots of brome growing with Senecio and Rudbeckia show no significant differences, 13.85 and 13.10 cm, respectively (Table 38). Brome roots growing with Senecio are significantly larger than roots of brome growing alone (11.60 cm). Between brome with Rudbeckia and brome alone, there are significant differences. An explanation for the good root development of brome growing with Senecio could be a soil effect. Usually Senecio and Rudbeckia growth where the soil is deep and mountain brome grows alone in the areas where the soil is shallow and rocky. However, even in the same soil, roots of brome with Senecio are more extensive than roots of brome with Rudbeckia, because as mentioned above, light competition forces brome growing with Rudbeckia to have a greater shoot development and this restrains root length.

Table 37. Differences in the average length of stems per plant of Mountain brome grass as affected by growing in association with *Rudbeckia occidentalis* with *Senecio serra* and alone

Replication	Treatment		
	Brca-Sese	Brca-Ruoc	Brca
	Length of stem in centimeters		
1	77	100	103
2	105	113	95
3	77	99	84
4	102	99	78
5	108	100	98
6	92	107	115
7	91	103	102
8	105	66	114
9	85	106	95
10	99	122	85
11	77	84	100
12	61	109	100
13	78	106	105
14	83	94	92
15	87	116	85
16	69	115	117
17	89	117	99
18	81	96	102
19	95	111	63
20	97	86	74
Average	87.90	102.45	95.30
	b*	a	a b

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

Table 38. Differences in the average length of roots per plant of Mountain brome grass as affected by growing in association with Rudbeckia occidentalis with Senecio serra and alone

Replication	Treatment		
	Brca-Sese	Brca-Ruoc	Brca
	Length of root is centimeters		
1	15	12	8
2	14	16	9
3	16	14	11
4	13	13	12
5	12	10	12
6	13	13	13
7	12	12	15
8	15	10	12
9	12	17	11
10	13	14	12
11	13	13	11
12	14	12	10
13	19	12	9
14	11	12	12
15	16	12	10
16	7	12	14
17	13	16	14
18	17	16	14
19	20	15	9
20	12	11	14
Average	13.85	13.10	11.60
	a *	a b	b

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

A better index for evaluating brome plant development is shoot/root weight ratio, because this ratio takes into consideration the different number of stems per plant and, also, differences in root development according to the age of the plants. There are no significant differences among the three treatments, so we can conclude that growth of mountain brome grass, especially root development, is not affected by inhibitory action of coneflower plants (Table 39).

An explanation for the apparent inhibition of coneflower leachate over the percent germination and root development of seeds of different species might be that of the water potential in the germinating medium. As the leachate concentration increases, the water potential will be more negative by the addition of solutes, creating a condition that may restrict the seeds in absorption of water for normal germination. Enhanced microbial activity is an alternate interpretation of the leachate effect.

In the case of germinating seeds, the new roots are more susceptible to this abnormal condition, which prevents their development.

Clipping and Carbohydrate Studies

Concurrent with the phenological studies, tests were made to determine basic principles regarding the nature and extent of the synthesis and storage of total non-structural carbohydrates under controlled clipping. R. occidentalis plants were clipped at different stages of their normal growth cycle.

Moisture content is high at the beginning of plant growth (rosette) and decreases as the season progresses (Figure 21), reaching the lowest value at

Table 39. Differences in the shoot/root weight ratio per plant of Mountain brome grass as affected by growing in association with *Rudbeckia occidentalis*, *Senecio serra* and alone

Replication	Treatment		
	Brca-Sese	Brca-Ruoc	Brca
	Air-dry shoot/root weight ratio		
1	2.45	2.73	2.36
2	4.00	2.50	4.58
3	3.08	2.50	1.80
4	3.30	1.24	3.55
5	3.20	2.00	0.90
6	2.45	0.84	3.63
7	2.91	3.17	3.67
8	3.33	1.80	2.05
9	10.00	1.50	4.25
10	1.00	4.17	2.00
11	0.89	2.38	3.26
12	0.72	1.80	2.42
13	2.50	0.70	2.00
14	10.00	0.94	1.60
15	1.32	2.00	4.50
16	1.88	6.00	5.37
17	2.38	1.27	7.00
18	1.63	5.00	1.90
19	5.00	2.50	0.37
20	3.44	6.66	0.62
Average	3.27	2.59	2.89
	a*	a	a

*Values accompanied by different letters are significantly different at the 5 percent level (Duncan Test).

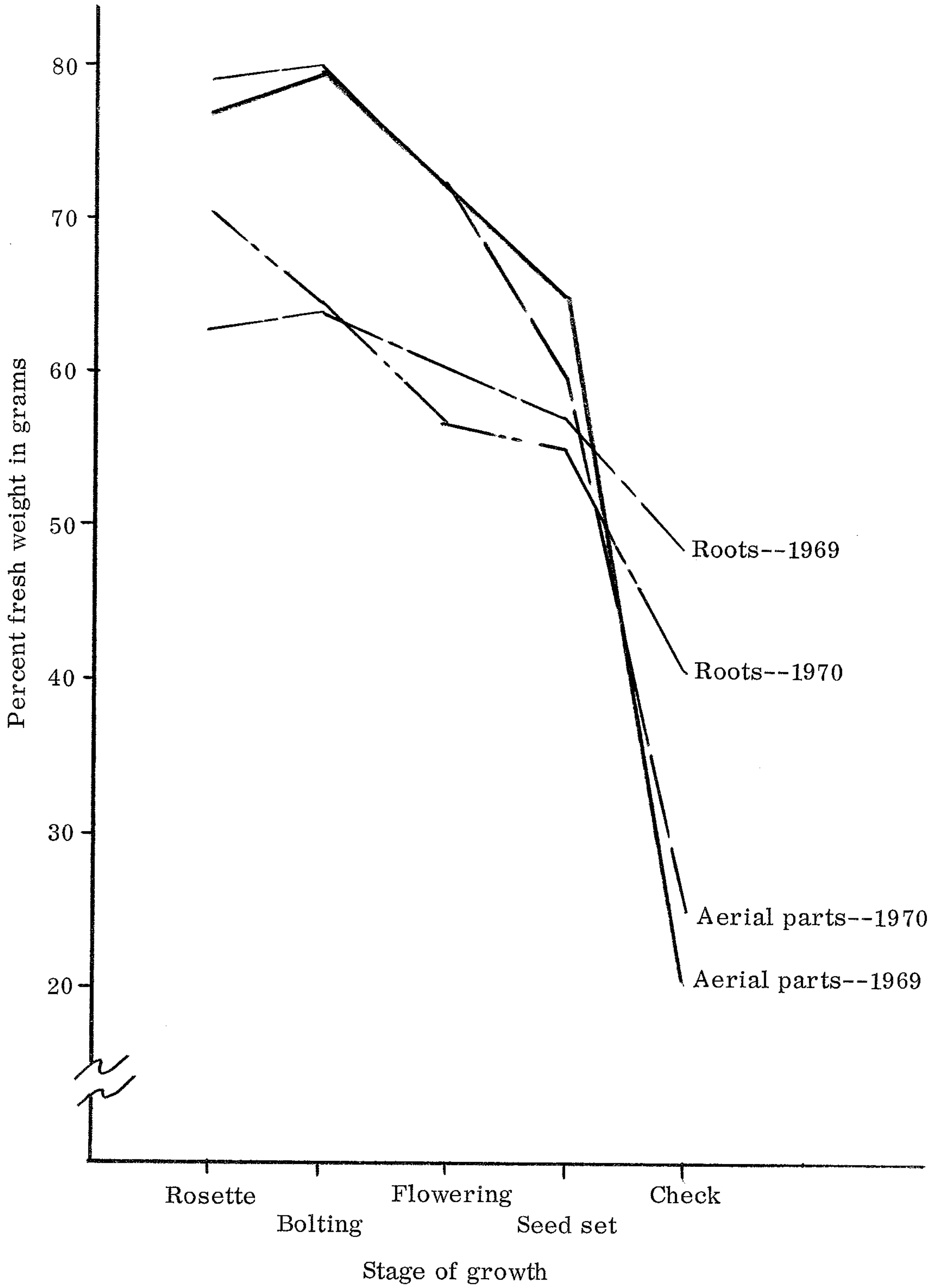


Figure 21. Seasonal trend of the percent fresh weights of average plants of Rudbeckia occidentalis clipped a single time at different stages of seasonal growth--1969-1970.

the end of the season as compared to the check plants. The reverse situation was true for dry matter yield, which was high at the end of the season and low at the beginning of the season when plants were in the rosette stage.

Clipping coneflower plants at the rosette stage resulted in death of three out of four plants after the third cut (Figure 22). The remaining one was dead after the second cut during the 1969 year. In 1970 one plant was dead after the fourth cut, one after the third cut and two remaining plants were alive after the fourth cut and before the winter season (Figure 23). At the bolting stage two cuts were possible during each of the seasons, 1969 and 1970, and only one cut was possible for the stages of flowering, seed set and check plants.

Dry matter yield per plant was greater at the end of the season for check plants than for the other growth stages even when the three or four harvests at the rosette stage are added together.

Analysis of variance of dry matter yields shows statistically significant differences by the F test at the 1 and 5 percent levels among stages of growth, year x stages interaction, and replications (Table 40). Yields (ADM) were significantly larger at the 5 percent level for the check plants, and in successive significant order for seed set over flowering, flowering over bolting and bolting over the rosette stage. No significant differences were obtained between years.

The influence of environmental conditions over the development of plants year by year is largely responsible for the significant interaction of stages of growth x years. Replications were significant because the plants studied were different in age, number of stems, height, etc.

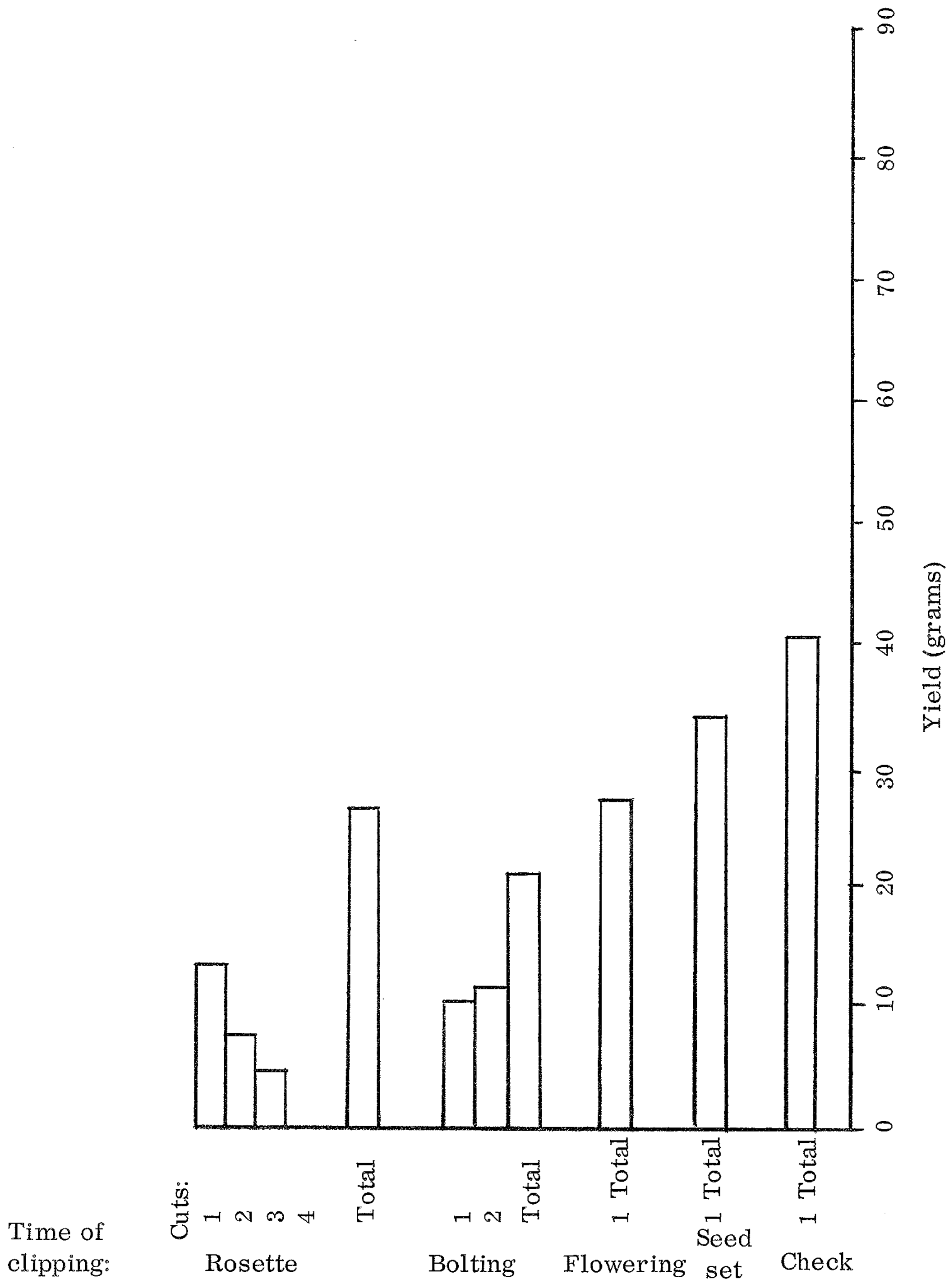


Figure 22. Yields expressed in grams of dry weight from clippings at different stages of seasonal growth on Rudbeckia occidentalis, 1969.

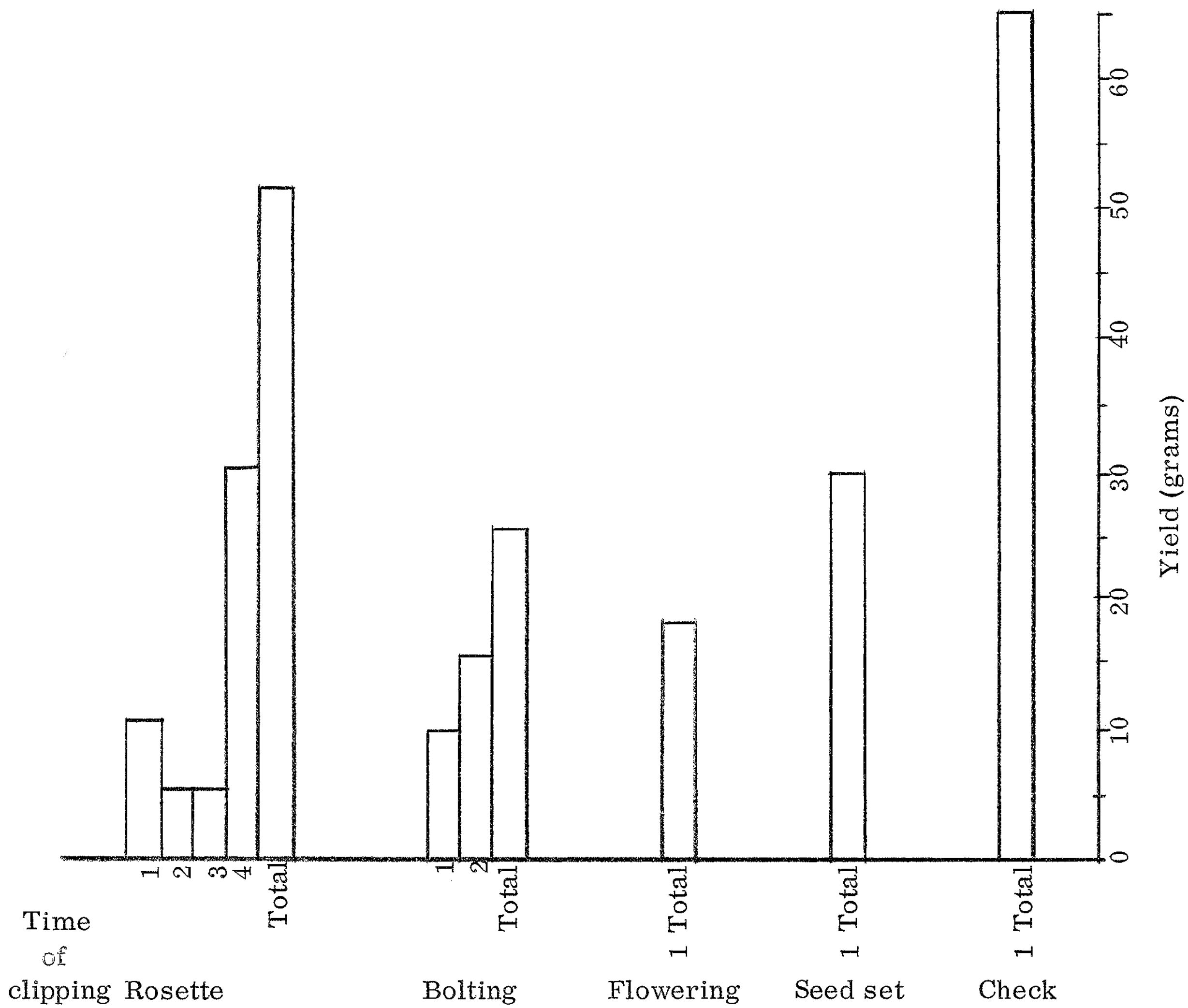


Figure 23. Yields expressed in grams of dry weight from clippings at different stages of seasonal growth on Rudbeckia occidentalis, 1970.

Table 40. Analysis of variance and comparison of the average dry matter yields by the Duncan's Test of plants of *Rudbeckia occidentalis* clipped during 1969-1970 at different seasonal stages

A. Dry matter yields--1969-1970

		A N O V A			
Source of variation	D. F.	S. S.	M. S.	F	Significance
Stages of growth	4	17,975.86	4,493.96	1,370.10	**
Years	2	5.38	5.38	1.64	
Stages x years	4	128.43	32.10	9.78	**
Replications	3	49.11	16.37	4.99	**
Error	27	88.70	3.28		
Total	39	18,247.48			

B. Comparison of the averages by the Duncan's Test

1. Average yields of 1969-1970

Stage	Av. D. M. Y. in grams	Duncan's Test
Rosette	11.94	e
Bolting	10.04	d
Flowering	18.02	c
Seed set	27.56	b
Check	67.64	a

2. Average comparisons by years

Year	Av. D. M. Y. in grams	Duncan's Test
1969	27.41	a
1970	26.67	a

The initial growth of a plant each year is dependent upon a source of carbohydrate reserves. These reserves also supply needed constituents for respiration and metabolic processes, including the synthesis of protoplasm, organic acids, cellulose, and nitrogenous compounds (Devlin, 1966).

With the onset of new growth there is, universally, a decline in stored carbohydrates (Jameson, 1963). The decline of reserves during early growth is well known. However, rate and time of the carbohydrate low may vary widely among species. The early period of growth produces a rapid increase of photosynthetic tissue requiring an increased utilization of carbohydrate reserves. Mooney and Billings (1960) reported on the carbohydrate cycle for alpine plants. A high carbohydrate level in the underground organs was depleted rapidly by developmental activity under the snow pack and with the onset of early shoot growth, followed by a rapid accumulation of reserve material which reached a plateau prior to fall dormancy.

Carbohydrate studies during 1969 for the rosette stage showed an average content of total available non-structural carbohydrates (TNC) of 6.20 percent for the aerial parts and 4.10 percent for the roots (Figure 24). As the season progressed, TNC in the aerial parts increased to 10.82 percent for the bolting stage, 9.77 for the flowering and 12.25 percent for the seed setting stage. Then a decrease was found in the check plant at the end of the season, with 7.40 percent TNC. Roots showed different trend, increasing to 4.75 percent in the bolting stage, 6.05 percent in the flowering stage and 11.05 percent in the seed set stage. However, instead of decreasing thereafter as in the

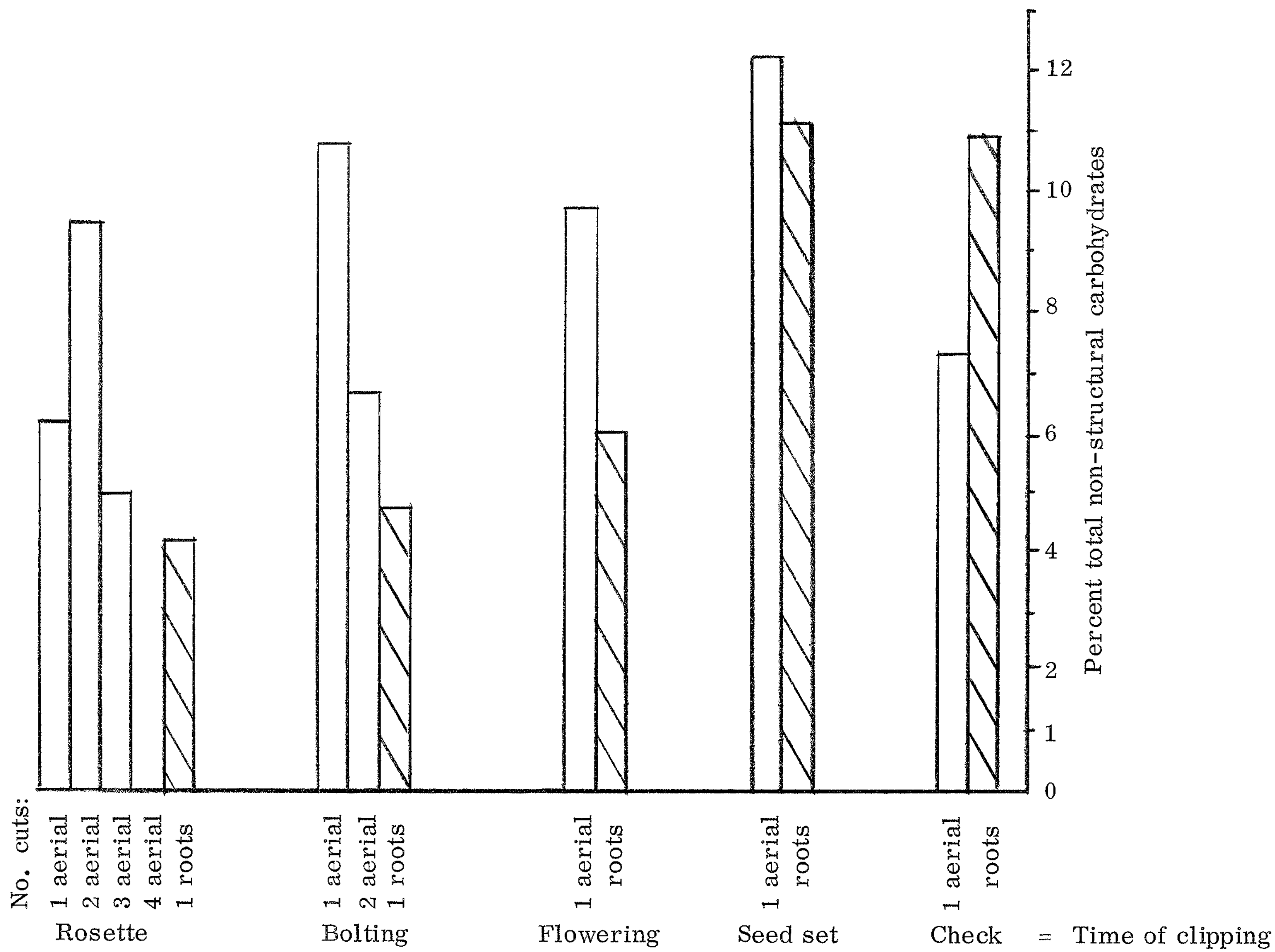


Figure 24. Average percent total non-structural carbohydrates from clippings at different stages of seasonal growth on Rudbeckia occidentalis, 1969.

aerial parts, the roots showed an increase to 10.85 in the check plant at the end of the season. A similar trend was found during 1970 (Figure 25) both for the aerial parts and the root. Proof of this is the lack of statistical significance between years 1969 and 1970 (Table 40). A graph representing these trends for the aerial parts and the roots for both years is shown in Figure 26.

TNC content by stages of growth for the aerial parts is shown in Table 41. The lowest significant percent of TNC corresponds to the rosette stages and the second lowest was in the check plants at the end of the season. Plants in the bolting, flowering and seed setting stages showed no significant differences in TNC but these stages were significantly higher than the other stages which clearly was a result of the photoysnthetic build-up. Comparing TNC content of roots the significantly higher contents of TNC were found in the seed set and check plants (Table 42). No significant differences in TNC were found among the rosette, bolting and flowering stages, but these stages were significantly lower than the other stages. Apparently a build-up in the TNC of the roots started after the flowering stage, when the aerial parts showed the lowest TNC contents. When plants were clipped every time they attained the rosette stage, less foliage was produced and there was less stored carbohydrates in their roots. Close clipping disrupts the natural growth processes and lengthens the vegetative period. At the same time new growth is stimulated which draws upon the carbohydrate already stored and reduces the total stores present. If the clipping continues available carbohydrate will be reduce to a critical level and the plant will be unable to regrow and ultimately will die. This was the case with clipping at the rosette stage (Figures 24 and 25).

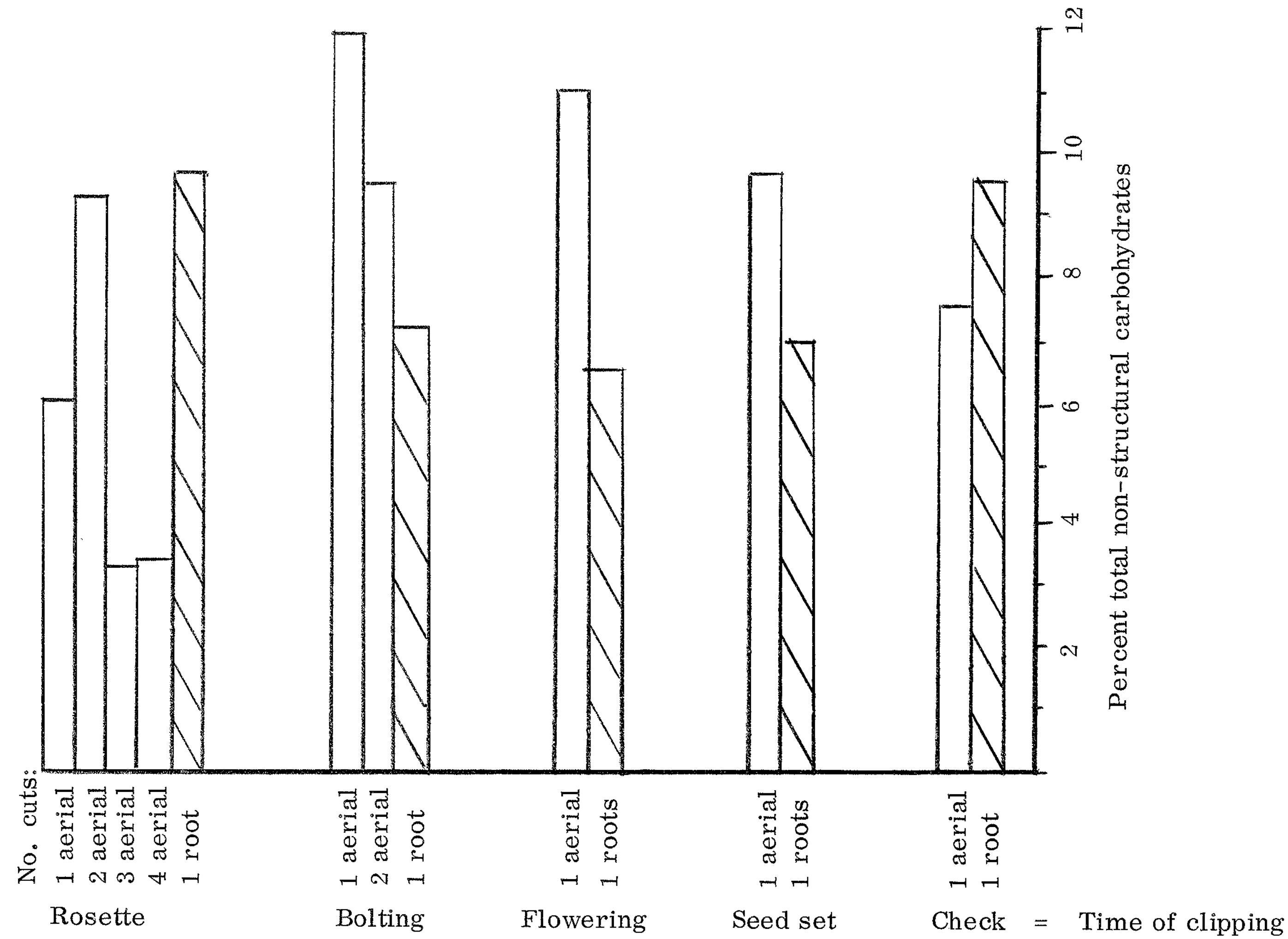


Figure 25. Average percent total non-structural carbohydrates from clippings at different stages of seasonal growth on Rudbeckia occidentalis, 1970.

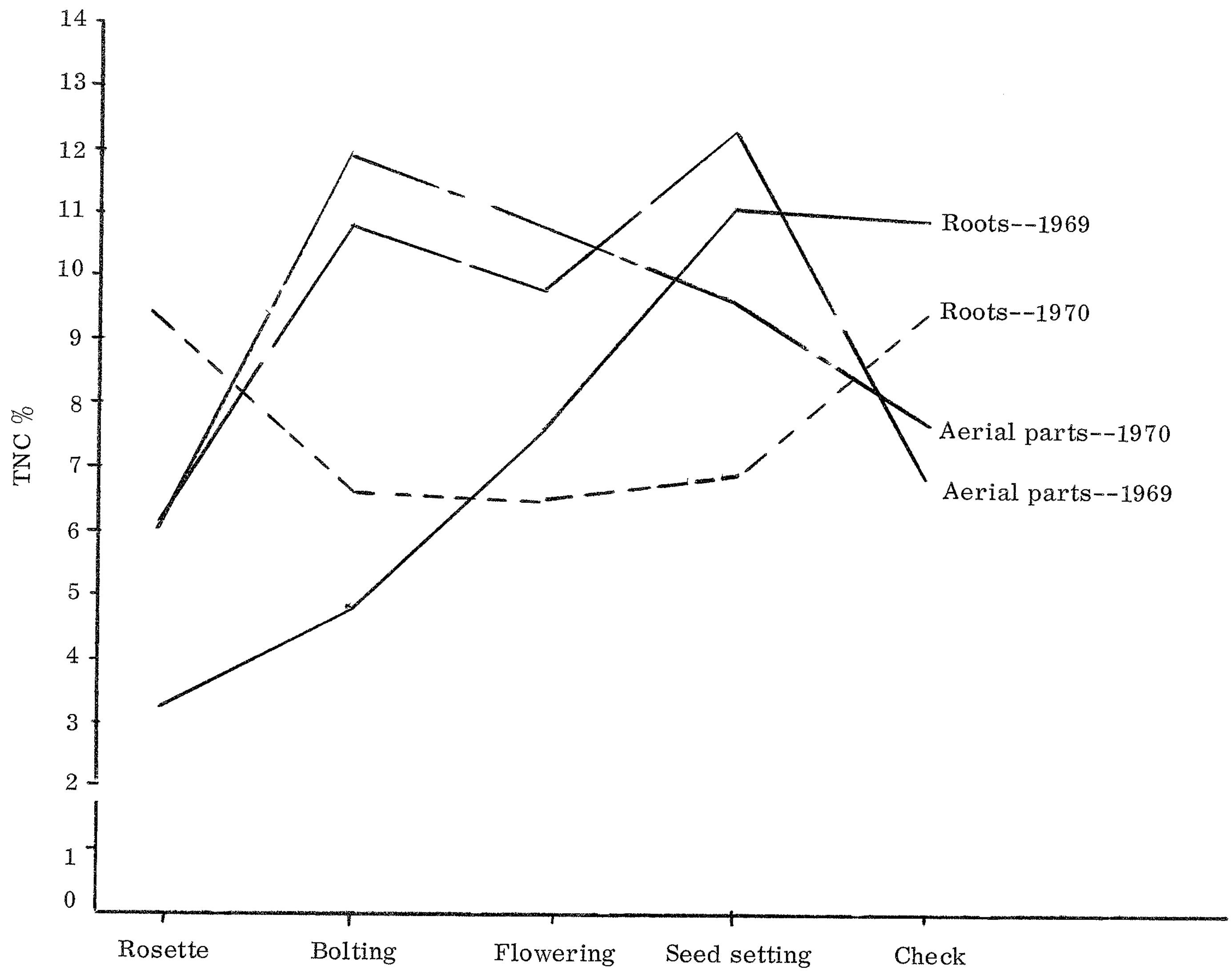


Figure 26. Trends of average non-structural carbohydrates at different stages of growth in plants of <u>Rudbeckia occidentalis</u>, 1969 and 1970.

Table 41. Analysis of variance and comparison of the average percent total non-structural carbohydrates content of aerial parts of plants of *Rudbeckia occidentalis* by the Multiple Duncan's Test--1969-1970

A. Percent TNC content--1969-1970

		A N O V A			
Source of variation	D. F.	S. S.	M. S.	F	Significance
Stage of growth	4	167.81	49.95	38.13	**
Years	1	0.11	0.11	0.10	
Stage x year	4	18.27	4.56	4.14	**
Replications	3	2.91	0.97	0.88	
Error	27	29.77	1.10		
Total	39	218.87			

B. Comparisons of the averages by the Duncan's Test

1. Average percent TNC of 1969-1970

Stage	Percent TNC	Duncan's Test
Rosette	6.12	c
Bolting	11.36	a
Flowering	10.29	a
Seed set	10.95	a
Check	7.59	b

2. Average comparisons by years

Year	Percent TNC	Duncan's Test
1969	9.29	a
1970	9.24	a

Table 42. Analysis of variance and comparison of the average percent total non-structural carbohydrates content of roots of plants of Rudbeckia occidentalis by the Multiple Duncan's Test--1969-1970

A. Percent TNC content--1969-1970

		A N O V A			
Source of variation	D. F.	S. S.	M. S.	F	Significance
Stage of growth	4	58.00	14.50	21.00	**
Years	1	0.97	0.97	1.40	
Stage x years	4	49.68	12.42	18.00	**
Replications	1	2.64	2.64	3.82	
Error	9	6.28	0.69		
Total	19	117.57			

B. Comparison of averages TNC by the Duncan's Test

1. Average percent TNC of 1969-1970

Stage	Percent TNC	Duncan's Test
Rosette	6.75	b
Bolting	5.68	b
Flowering	6.31	b
Seed set	9.00	a
Check	10.15	a

2. Average comparisons by year

Year	Percent TNC	Duncan's Test
1969	7.36	a
1970	7.80	a

The content of TNC at the same stage was lower each time after the first cut for the aerial parts. After three or four cuts the plants died. Analysis of roots of dead plants showed (Table 43) an average TCN of 2.15 percent for 1969 and 1.37 percent for 1970. This suggests that even though carbohydrates are important for regrowth of plants there are other controlling factors that could be as important as availability of carbohydrates. It was observed in the field after the first cut in the rosette stage that Rudbeckia plants form new buds in the crowns toward the end of the snow-free period. Some of these buds and older ones produce the first shoots and leaves in early spring for the rosette stage. If clipped at this time a new rosette with less foliage will be formed at expense of the remaining buds. Production of foliage following another clipping will be conditional on the availability of new buds, otherwise the plant will die. During 1969 three out of four plants died after the third cut at the rosette stage and the remaining plants died after the second cut. The average TNC content of the roots of those dead plants showed a total of 2.15 percent. During 1970 two out of four plants died after the fourth cut, and the remaining plants remained alive. The TNC content of the roots of dead plants showed an average of 1.37 percent. Visual inspection of the roots and crowns showed no more available buds.

In the bolting stages, two cuts per year appeared to reduce the TNC content in the aerial parts of the plants but they remain alive. In subsequent stages only one cut was possible.

Table 43. Average total non-structural carbohydrate in percentage of the roots of death plants of Rudbeckia occidentalis after several clippings were done in the rosette stage of seasonal development

Stage of growth	Replication	No. of clippings before death 1969	1970	T.A.C. of root of death plant 1969	1970	T.A.C. of root before clippings 1969	1970
Rosette	1	4	4	4.80	1.05		
	2	4	3	1.50	1.70		
	3	3	Alive	0.50			
	4	4	Alive	1.80			
	Average			2.15	1.37	4.10	9.40

Figure 27 shows the annual herbage growth of R. occidentalis in relation to the trend of root and stem-base storage of carbohydrates for the year 1935-1936. This research was conducted by McCarty and Price (1942). A similar trend in the reducing sugar content of plants as the season progressed was found in this study. Important highlights of the McCarty and Price study shows that R. occidentalis differs outstandingly from grasses in carbohydrate storage in the roots and stem bases in that it has:

1. An abrupt beginning and a rather brief duration of carbohydrate storage,
2. Storage of greater quantities of carbohydrates in the roots,
3. Higher starch values, and
4. Lower hemicellulose values.

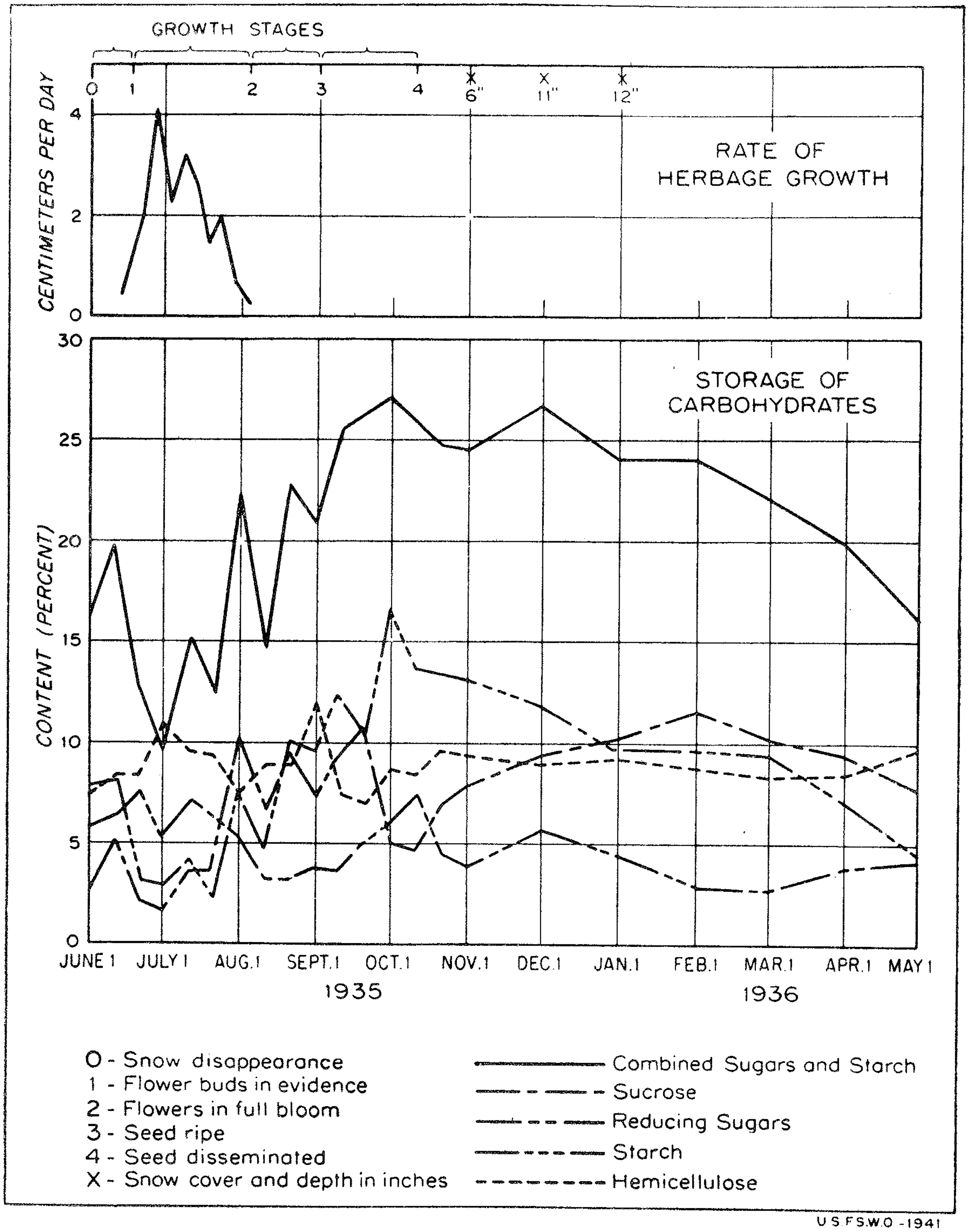


Figure 27. Annual herbage growth of Rudbeckia occidentalis in relation to the trend of root and stem-base storage of carbohydrates, 1935-36 (McCarty and Price, 1942, p. 18).

These differences result chiefly from differences in growth habits. The fact that broadleaf plants produce large quantities of photosynthetic tissue within a comparatively short period would condition the time and manner of storage. The presence of large quantities of starch in the roots appears to be related to the production of large fibrous taproots.

McCarty and Price (1942) also found that the minimum concentration of total sugars and starch in roots and stem bases of Rudbeckia was 9.73 percent in 1935. The maximum concentration in the same was 27.78 and the time required for this change was 91 days, from July 3 to October 2.

Chemical Analysis

Samples of Rudbeckia occidentalis were sent to the Industrial Laboratories Company of Denver, Colorado, for proximate chemical analysis when the plants were between the bolting and flowering stages. The samples were composites of the entire aerial portions. The samples were collected in an area at 7,800 feet elevation in the Centennial Mountains at the U.S. sheep experiment station summer range, Montana, where about 2 percent of the vegetation was constituted by Rudbeckia. The results of the analysis are reported in Table 44. Samples from July 19, 1968, may have been dried at too high a temperature, therefore, fiber and lignin could be in error.

As is the case with many plant species protein in Rudbeckia is higher at the beginning of regrowth and decrease as the season advances. On July 19 it was 14 percent and decreased to 9.1 percent by August 27, 1968. Also,

Table 44. Chemical analysis of Rudbeckia occidentalis sampler in percentages during 1968

Date	Stage	Air dried sample Moisture	Ash	Protein	Ether extract	Acid detergent fiber	A-D lignin
July 19	Bolting	9.1	11.1	14.0	2.9	34.7	10.6
Aug. 2	Flowering	8.1	8.4	11.9	2.1	29.6	7.9
Aug. 10	Flowering	8.8	8.0	10.2	1.8	35.0	7.6
Aug. 27	Seed set	8.9	8.0	9.1	2.1	28.9	9.5

lignin shows the reverse trend, being higher at the end of the season at 9.5 percent.

Toxicity Studies

At the Poisonous Plant Research Laboratory, U.S.D.A. in Logan, three ewe sheep were fed Rudbeckia occidentalis in the form of dried and ground material by pumping it into the rumen, beginning August 31, 1970.

Sheep No. 1971 was fed with 453 grams of ground material each day for 4 days. Sheep No. 1917 was fed 302 grams the first day and because no toxicity symptoms were observed on the second day the doses were raised to 604 grams daily for 3 days. Sheep No. 1976 was fed 151 grams the first day but, since again no symptoms of toxicity were observed, the doses were raised to 604 grams daily for 3 days.

After a careful daily inspection of each animal during the 4 days of the trial no symptoms of toxicity were observed due to the ingestion of R. occidentalis material into the rumen, even though the doses were high for this kind of trial. The conclusion is that no immediate toxicity is presented by feeding coneflower to sheep when the plant is at the seed set stage during the season when the Forest Service allows summer grazing in aspen areas each year. Even if symptoms of toxicity can be observed on a long term basis they are certainly not on a short term basis.

SUMMARY AND CONCLUSIONS

The study was conducted during 1968, 1969, and 1970 in the Wasatch Mountains (Bear River Range) of Northern Utah. Three exclosures were located on aspen range in Tony Grove Canyon about 25 miles to the northeast of the City of Logan. The specific objectives were to study the taxonomy, morphology, phenology, developmental history, ecological and physiological relationships of Rudbeckia occidentalis.

Although all soils in the study area are typed as loams (based on the surface soil texture) there is considerable variation in texture of the different horizons. Because of the occasional rains during the growing season the moisture availability was not a problem for the growing plants.

According to the United States Weather Bureau precipitation map, the experimental area lies in the 25 inches annual precipitation zone, most of which is received in the form of snow. The mean annual temperature for the area is 37 F, with a July mean of 62 F and a January mean of 20 F. The average frost-free period in the aspen zone is 85 days and is usually from June to September.

R. occidentalis, or Western coneflower, is a coarse perennial herb of the aster or sunflower (Compositae) family.

Results of phenologic studies of mature plants of coneflower showed that growth began as soon as snow melted and the temperature continually rises. In 1969 and 1970 the rosette stage was attained on May 29 and June 11, respectively, a difference of 13 days. The condition of late snow melt and low temperature associated with it created this time lag of about 2 weeks. Temperature appeared to constitute a limiting factor for the rosette stage.

The next stage, bolting, is mainly characterized by a rapid growth of the stems and occurred in both studied years at about 1 week after the completion of rosette growth. For 1969 the rate of stem growth in this period was of 3.66 cm daily and 3.88 cm daily for 1970, constituting the highest rate of growth for the entire life cycle of coneflower.

By July 18, 1969, and July 28, 1970, 10 percent of the heads of coneflower had their flowers opened and almost 1 week later, 50 percent of flowering was attained and 100 percent flowering was reached by July 28, 1969, and August 13, 1970. The flowering stage is characterized by the presence of the flower head which usually has a short conic to columnar form and develops solitary on long penduncles at the end of stems or stem branches. Apical dominance is present. Cross-pollination occurs 97 percent of the time.

The seed-setting stage was initiated by August 14, 1969, and August 20, 1970, almost a lag of 1 week between 1969 and 1970. By August 25, 1969, and August 30, 1970, all the plants with heads completed the seed formation process and dissemination was started and completed by September 15, and 17 during both years--1969 and 1970.

Dissemination of coneflower seeds is mainly by gravity but the distribution around the mother plant depends entirely upon the wind action. Therefore, the direction of dissemination is influenced by the degree to which the wind blew and the direction. The results of dissemination studies in 1969 and

1970 were similar, and it is important to mention that in most of the plants studied, the seeds were more prevalent close to the mother plant.

Phenological studies of Rudbeckia seedlings during 1969 and 1970 showed that the mean density of live seedlings decreased as the season advanced as the season advanced. This decrease in seedling survival reached the maximum value during the period of July 20 to July 12 in 1969 and from June 18 to June 25 in 1970, probably due to the competition produced by the rapid growth of older associated species. Also, climatic conditions have a great influence on survival of seedlings. In 1969 a late snow produced an increase in the seedling mortality at the end of June. At the end of the growing season in 1969, 51 percent of the seedlings were alive, in contrast with 1970 when 60 percent were alive. This difference is mainly the effect of a late snow in 1969. In both years, seedling growth was restricted to the development of one stem which reached an average height of 4.85 cm for 1969 and 5.61 cm for 1970. During both periods only one to three leaves were developed on the stem. However, even then the seedling did not develop very much during their first year and remained small. The shoot/root weight ratio indicated that the main development during this stage of life was in the root.

Two year old seedlings showed a different behavior than in their first year of growth. Height attained was on the average 22.10 cm by July 9. The number of leaves increased and also were larger than during the first year growth. Also, the root attained a great development, reaching a shoot/root weight ratio of 1 to 3.27. At this stage on the life cycle of coneflower, however, the plants still maintained their rosette form without bolting. In general, only plants 4 years old bolted, flowered and produced seed. The first 3 years of growth is devoted to root and bud development.

Studies of seeds of R. occidentalis, collected from the Tony Grove area, showed that size of the seed is not important in the germination of this species, and that large seeds germinate as easily as small seeds under optimum conditions.

Optimum conditions for seed germination were found to be alternating temperatures of 25 C-15 C and 8 hours light, coinciding with the higher temperature. Constant temperatures and light or alternating temperatures and darkness gave significantly lower germination percentages.

The percentage of filled seeds in heads reflected how favorable the environmental conditions were after the flowers were pollinated. In order to know these influences in different sites in the State of Utah, collection of seeds of individual plants were made in different places during 1969 and 1970. The results showed large differences in percent germination among places that are difficult to explain with the limited knowledge available for this study. However, it appears that altitude has an important effect in the production of viable seeds. Seeds from high altitude at Ephraim (10,400 feet) had very low germination, 1.33 and 0.0 percent, in comparison with seeds from the same area but lower altitude (8,800 feet) with a better germination percent: 44.0 and 46.6. Staining the seeds of these areas with 2,3,5-triphenol-2H-tetrazolium chloride showed that all filled seeds from these collections gave positive reaction. So, the conclusion was that seeds from higher elevations failed to fill.

Relative gopher populations in the study area were determined by counting the current year's mounds and estimating the gopher population. An upward trend in gopher population or general burrowing activity occurred in 1970 from that in 1969. One of the reasons for this increase could be due to soil moisture which was higher in 1970 than in 1969.

It is certain that pocket gophers affect the growth and composition of coneflower in areas such as Tony Grove where it is one of the dominant forbs. However, the specific effect of feeding and burrowing on plant development and changes in composition needs more investigation.

At the time of seed set during August and September R. occidentalis is heavily infected by powdery mildew in the field. The disease is caused by the fungus Eyrsiphe cichoracearum DC. Field observation indicate a relationship between leaf growth and mildew development. Examination of plants has shown that only those in which leaf growth has ceased were these signs of the disease. Younger plants showed less infection or no symptoms at all in the case of new rosettes. By application of gibberellic acid (GH_3) solution as a leaf spray to promote regrowth after clipping, the above assumption about younger plants was tested.

The results showed that when the leaves have ceased growth they are most susceptible to mildew attack. However, some mildew symptoms may appear even if the leaves are growing.

Field observations showed that some Rudbeckia plants went without bolting and flowering throughout the growing season and yet showed vigorous growth. It was believed that some kind of fertilization (for example, by livestock manure) was responsible for it, especially with respect to nitrogen. Application of an equivalent of 40 kgs x Ha of ammonium sulfate (21 percent) to plants growing in the greenhouse in soil from the Tony Grove area maintained the plants in the rosette stage while plants without nitrogen application during the same period of observation went from rosette to bolting and ultimately to flowering. The speculation on these results as applied to field conditions is that when some plants are supplied with nitrogen (livestock manure), vegetative growth in the rosette stage is prolonged. Then when plants are ready to go to the next stage adverse environmental conditions such as low temperature or short photoperiod may inhibit it, so that the plants remain in the rosette stage until the next season.

Flowering in R. occidentalis is not the result of a series of autonomous processes determined solely by the genetic constitution but is controlled by environmental factors which interact with the genetic constitution in a specific manner. The two climatic factors which play by far the most important rate in controlling flower development are temperature and day length.

The results of placing a set of plants with and without cold treatment under 12 hours of photoperiod and another similar set under 18 hours photoperiod under growth chamber conditions with alternating temperatures of 25 C-15 C (16 hours-8 hours) showed that only those plants under long photoperiod (18 hours) produced flowering while those under 12 hours of light remained in the rosette stage. Plants with and without cold treatment produced flowering under long photoperiods, indicating that cold treatment is not required for the flowering process.

Leaf area under long photoperiod (18 hours light) was not significantly different between plants subjected to cold treatment and plants without it. On the other hand, under short photoperiod (12 hours) when Rudbeckia plants remain in the rosette stage, cold treatment has an interesting effect in the leaf area development. Leaves without cold treatment are significantly smaller than leaves with cold treatments.

As Salisbury and Ross (1969) said, an important positive response of plants to low temperatures is the effect of low temperature upon the vegetative forms and growth of certain plants. We are concerned mostly with inductive (delayed) effects upon some developmental plant process. Such effects may also be observed in response to the length of the day and perhaps to other environmental factors as well. In fact, low temperature and day length effects are frequently interrelated, but some physiological mechanisms are difficult to explain at the moment. Here could be the explanation of why leaves without cold treatment are smaller than leaves with cold treatment under short photoperiod.

Similar results were obtained under growth chamber conditions and greenhouse conditions. Plants under long photoperiods, irregarless of the cold treatment, bolted, flowered, and set seed. There were no differences in terms of leaf area between the plants with and without cold treatments.

Plants under natural greenhouse conditions (short winter photoperiod) remained in the rosette stage irregardless of cold treatment. However, the leaf area in the plants with no cold treatment was smaller than the leaf area of plants with cold treatments.

Plants showed extreme plasticity, responding remarkably in size and form to environmental conditions. One of the most potent of these external forces is the pressure of competing neighbors which may reduce a plant to diminutive size. When plants 2 years old are widely spaced (20 x 20 cm) under favorable conditions of water, light and nutrient supply so that no competition occurred between them, they continued to grow at a nearly constant rate until they passed from the vegetative (rosette) stage to bolting, flowering and finally to seed production. In contrast, plants entering into early competition (5 x 5 cm spacing) with their neighbors immediately showed a reduction in growth which became progressively more marked as competition intensified, so that the plants remained in the vegetative stage.

Apparently, in close spacings, competition for light is not immediately one of competition among plants. It is competition between leaves. If one leaf lies above another as was the case with the close spacings, then the depression of the photosynthetic rate of the lower leaf will be the same, whether the superior leaf is of the same plant or another. This competition between leaves was especially evident in the dense treatment at 5 x 5 cm and partially evident in the 10 x 10 cm spacing.

During the first year of the competition studies, no signs of competition were observed among the spacing treatments. The major differences were in the vigor and percentage survival of seedlings 2 weeks old that had been germinated in petri dishes in the laboratory and started in the greenhouse, compared to similar treatments using seeds directly seeded in the field. Before the snow cover developed (December, 1969), survival from transplanting was 100 percent, while in the seeded treatments it was 40 percent. Those seedlings (2 weeks old) that were germinated under optimum conditions in the growth chamber were able to cope better with the environmental conditions when transplanted to the field than the seedling that emerged from seeds planted directly in the field.

Since Carnahan and Hull (1962) reported inhibitory effect of _R. occidentalis_ on intermediate wheatgrass and radish, several studies were undertaken to determine whether there were specific inhibitory substances in _Rudbeckia_ and whether these inhibitory substances were toxic to seed germination of other species.

Since various concentrations of _Rudbeckia_ leachate may occur in the soil in the field, it was important to have a standard concentration as a basis for all experiments and to determine which dilutions, if any, inhibit the germination of seeds and the growth of seedlings. Throughout the experiment there was a general trend for the higher concentrations of leachate to increase the inhibitory effects upon the germination of the seeds of Manchar smooth brome grass and Nordan wheatgrass. In the germinated seeds, leachate concentrations produced abnormal growth in the seedlings, especially in root development.

Attempts to isolate specific inhibitory substances from Rudbeckia material were undertaken. Leachate boiled for 5 minutes and tested on germinating seeds of Nordan wheatgrass showed that the inhibitory substance was not destroyed or inactivated but rather appeared to be more inhibitory than the unboiled leachate. When activated charcoal (Norit A) was added to the leachate and the suspension filtered and centrifuged before use, it showed the same inhibitory activity on the germination of the wheatgrass seeds. Leachate dialyzed against distilled water for 24 hours appeared not to be as inhibitory as the original undialyzed leachate on the germination of wheatgrass seeds. Leachate kept in a refrigerator for several days showed a similar inhibitory effect on the percent germination and root development of Nordan wheatgrass seeds. Chromatography studies using Rudbeckia extract with distilled water, buthanol, or 40 percent methanol as developing solvents gave similar results, except that a trace of buthanol which remained in the paper after air-drying apparently was inhibitory to the development of the few germinated seeds of Nordan wheatgrass. Both distilled water and methanol showed that the segment which inhibited root growth was in the range of RF 0.8-1.0.

To see if the results on inhibition were conclusive for Rudbeckia, similar trials, as reported, were done also with extract of tomato leaves and mountain bromegrass. In testing the effect of tomato leaf extract in different concentrations upon the germination of Nordan wheatgrass, results were similar to those obtained with Rudbeckia leachate. Mountain bromegrass gave similar results. Apparently from the results discussed above, the reduction in the percent germination and especially in root development is not due to the presence of specific inhibitors in the leachates used, but to other ecophysiological mechanisms, such as osmotic effects or microbial action. Alternatively, the leachates from a broad range of plants may be shown to contain growth inhibitory compounds when used in sufficiently high concentrations under laboratory conditions. These results cast some doubt on the validity of other published reports regarding the significance of specific allelopathic effects.

In order to determine if R. occidentalis produces inhibitors in the field which limits the growth of associated species, Mountain bromegrass (the principal associated species) was chosen as an indicator of such inhibitors. Plants of mountain brome were studied with regard to stem height, root length and shoot/root weight ratio in areas where it grew alone and in areas in which it grew associated with Senecio serra or Rudbeckia occidentalis. The results showed no inhibitory effects by Rudbeckia over the growth of Mountain bromegrass.

Concurrent with the phenological studies, tests were made to determine basic principles regarding the nature and extent of the synthesis and storage of total non-structural carbohydrates under controlled clipping. R. occidentalis plants were clipped at different stages of their normal growth cycle. Clipping Rudbeckia plants at the rosette stage resulted in death of three out of four plants after the third cut. The remaining one was dead after the second cut during the 1969 year. Similar results at the rosette stage were obtained during 1970.

At the bolting stage two cuts were possible during each of the seasons 1969 and 1970 and only one cut was possible for the stages of flowering, seed set and check plants.

The initial growth of a plant each year is dependent upon a source of carbohydrate reserves. In R. occidentalis plants carbohydrate studies during 1969 for the rosette stage showed an average content of total available non-structural carbohydrates (TNC) of 6.20 percent for the aerial parts and 4,10 percent for the roots. As the season progressed, TNC in the aerial parts varied from 10.8 percent for the bolting stage to 9.77 percent for the flowering and 12.25 percent for the seed setting stage. Then a decrease was found in the check plants at the end of the season with 7.40 percent TNC. Roots shown another trend, increasing to 4.75 percent in the bolting stage, 6.05 percent in the flowering stage and 11.05 percent in the seed set stage. However, instead of decreasing thereafter as in the aerial parts, the roots showed an increase to 10.85 in the check plants or end of the season. A similar trend was found during 1970.

When plants were clipped every time they attained the rosette stage, less foliage was produced and there was less carbohydrates in their roots. With repeated clipping available carbohydrates were reduced to a critical level and the plants were unable to regrow and ultimately died. The content three out of four plants after the third cut. The remaining one was dead after the second cut during the 1969 year. Similar results at the rosette stage were obtained during 1970.

At the bolting stage two cuts were possible during each of the seasons 1969 and 1970 and only one cut was possible for the stages of flowering, seed set and check plants.

The initial growth of a plant each year is dependent upon a source of carbohydrate reserves. In R. occidentalis plants carbohydrate studies during 1969 for the rosette stage showed an average content of total available non-structural carbohydrates (TNC) of 6.20 percent for the aerial parts and 4.10 percent for the roots. As the season progressed, TNC in the aerial parts varied from 10.8 percent for the bolting stage to 9.77 percent for the flowering and 12.25 percent for the seed setting stage. Then a decrease was found in the check plants at the end of the season with 7.40 percent TNC. Roots shown another trend, increasing to 4.75 percent in the bolting stage, 6.05 percent in the flowering stage and 11.05 percent in the seed set stage. However, instead of decreasing thereafter as in the aerial parts, the roots showed an increase to 10.85 in the check plants or end of the season. A similar trend was found during 1970.

When plants were clipped every time they attained the rosette stage, less foliage was produced and there was less carbohydrates in their roots. With repeated clipping available carbohydrates were reduced to a critical level and the plants were unable to regrow and ultimately died. The content of TNC at the rosette stage was lower each time after the first cut for the aerial parts. After three or four cuts the plants were dead. Analysis of roots of dead plants showed an average TNC of 2.13 percent for 1969 and 1.37 percent for 1970. This suggests that even though carbohydrates are important for regrowth of plants, there are other controlling factors that could be as important as availability of carbohydrates since some carbohydrates we left even in dead plants.

Proximate analysis of above ground plant material showed protein in Rudbeckia is higher at the beginning of the regrowth and decrease as the season advances. Lignin showed the reverse trend.

At the U.S.D.A. Poisonous Plant Research Laboratory in Logan, three sheep were fed R. occidentalis in the form of dried and ground material by pumping it into the rumen. No symptoms of immediate toxicity were obtained by feeding Rudbeckia to sheep when the plants were in the seed set stage, during the season when the Forest Service allows summer grazing in aspen areas each year.

LITERATURE CITED

Altman, P., and D. Dittmer. 1962. Growth including reproduction and morphological defelopment. Federation of American Societies for Experimental Biology, Washington, D. C.

Austin, J. P. 1938. Minimum intensity of artificial illumination effective in supplementing the normal photoperiod. Papers of the Michigan Academy of Sciences, Arts and Letters 22:25-26.

Battaglia, E. 1951. Development of angiosperm embryo sacs with non-haploid eggs. American Journal of Botany 38(9):718-724.

Blake, S. F. 1931. Nine new American asteraceae. Journal of Washington Academy of Sciences 21(14):325-336.

Bleak, A. T. 1961. Annual progress report: Range revegetation investigations. Crop Research Service, United States Department of Agriculture, Logan, Utah.

Buchanan, B. A. 1969. The life history and ecology of bur buttercup Ranunculus testiculatus Crantz. Unpublished MS thesis, University of Utah Library, Salt Lake City, Utah.

Cain, S., and G. M. de Oliveira Castro. 1959. Manual of vegetation analysis. Harper & Brothers, Publishers, New York.

Carnahan, G., and A. C. Hull, Jr. 1962. The inhibition of seeded plants by tarweed. Weeds 10(2):87.

Chailakhyan, M. K. 1957. The influence of Gibberellin on plant growth and flowering. Doklady Akademica, Nauk USSR (Translation from the Botany Science section). 117(1/6):291-295.

Chalk, L. 1944. On the taxonomic value of the anatomical structure of the vegetative organs of the Dicotyledons. Proceedings of the Linnaean Society at London 155(3):214-218.

Chestnut, V. K., and E. V. Wilcox. 1901. The stock poisoning plants of Montana. U. S. Department of Agriculture, Division of Botany. Bulletin 26:123.

Costello, D. F., and G. T. Turner. 1944. Judging condition and utilization of short-grass on the central great plains. United States Department of Agriculture, Farmer Bulletin 1949.

Daubenmire, R. 1953. Nutrient content of leaf litter of trees in the Northern Rocky Mountains. Ecology 34:786-792.

________. 1959. Plants and environment. John Wiley & Sons, Inc., New York.

Devlin, R. M. 1966. Plant physiology. Reinhold Publishing Corporation, New York.

Dress, W. 1961. Notes on the cultivated Compositae. VI. The coneflowers: Dracopis, Echinacea, Ratibida, and Rudbeckia. Baileya 9(2):67-83.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecology Monograph 24:89-184.

Forest Service, United States Department of Agriculture. 1937. Range plant handbook. U.S. Government Printing Office, Washington, D.C.

Garner, W. W., and H. A. Allard. 1927. Effects of short alternating periods of light and darkness on plant growth. Science 66(1627):40-42.

Gasto, J. M. 1969. Comparative autecological studies of Eurotia lanata and Atriplex confertifolia. Unpublished PhD dissertation, Utah State University Library, Logan, Utah.

Gates, F. C. 1930. Principal poisonous plants in Kansas. Kansas State Agriculture Experiment Station Technical Bulletin 25:66-67.

Gleason, H. 1958. The new Britton and Brown illustrated flora of the Northeastern United States and adjacent Canada. The New York Botanical Gardens, New York.

Greig-Smith, P. 1964. Quantitative plant ecology. Butterworth and Company, Washington, D. C.

Greulach, V. A. 1942. Photoperiodic after-effects in six Composites. Botanical Gazette 103(4):698-709.

Hansen, A. A. 1930. Indiana plants injurious to livestock. Indiana Agriculture Experiment Station Circular No. 175.

Harshberger, J. 1911. Phytogeographic survey of North America. G. E. Stechert & Company, New York.

Holland, E. D., Jr. 1952. Stratigraphic details of the lower Mississippi rocks of Northeastern Utah and Southeastern Montana. Bulletin of American Association of Petroleum Geologists 36:1697-1734.

Houston, R. 1954. A condition guide for aspen ranges of Utah, Nevada, Southern Idaho, and Western Wyoming. United States Department of Agriculture, Forest Service Research Paper No. INT-32.

Jameson, D. A. 1963. Response of individual plants to harvesting. Botanical Review 29:632-694.

Kearney, T., and R. Peebles. 1951. Arizona flora. University of California Press, Berkeley and Los Angeles.

Knowlton, G. F. 1942. Aphids from Mount Timpanogos, Utah great basin. Nature 3(1):5-8.

________. 1954. Aphids on Rudbeckia. Entomology News 65(1):16.

Knowlton, F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. The Journal of Wildlife Management 24:162-170.

Lingelsheim, A. 1928. Cumarin bei der gattung Rudbeckia. Ber. Deutsch. Botanical Gazette 46(9):593-594.

Matthews, V. B. 1965. An ecological life history of tall bluebell in Utah. Unpublished MS thesis, Brigham Young University Library, Provo, Utah.

McCarty, E., and R. Price. 1942. Growth and carbohydrate content of important mountain forage plants in Central Utah as affected by clipping and grazing. Technical Bulletin No. 818. United States Department of Agriculture, Washington, D. C.

Metcalfe, C. R., and L. Chalk. 1950. Anatomy of Dicotyledons. Clarendon Press, Oxford, England.

Mitchell, E. 1926. Germination of seeds of plants native to Dutchess County, New York. Botanical Gazette 81:108-112.

Mooney, H. A., and W. D. Billings. 1960. The annual carbohydrate cycle of alpine plants as related to growth. American Journal of Botany 47:594-598.

Murneek, A. E. 1936. A separation of certain types of response of plants to the photoperiod. Proceedings of the American Society of Horticultural Scientists 34:507-509.

Pammel, L. H. 1911. A manual of poisonous plants. The Torch Press, Cedar Rapids, Iowa.

Pelton, J. 1953. Ecological life cycle of seed plants. Ecology 34:619-628.

Piper, C. 1906. Flora of the State of Washington. Vol. 25. Contributions from the United States National Herbarium, Washington, D. C.

Richens, V. B. 1964. An evaluation of control on the pocket gopher Thomomys talpoides, on the Cache National Forest, Utah. Unpublished MS thesis, Utah State University Library, Logan, Utah.

Roberts, R. H., and B. E. Struckmeyer. 1938. The effects of temperature and other environmental factors upon the photoperiodic responses of higher plants. Journal of Agricultural Research 56:633-678.

Sadlick, W. 1955. Carboniferous formations of Northeastern Uintah Mountains. Wyoming Geological Association Guidebook.

Salisbury, E. J. 1929. The biological equipment of species in relation to competition. Journal of Ecology 17:197-222.

Salisbury, F., and C. Ross. 1969. Plant physiology. Wadsworth Publishing Company, Inc., Belmont, California.

Sampson, A. W. 1917. Important range plants: Their life history and forage value. United States Department of Agriculture Bulletin No. 545.

________. 1923. Our native broad-leaved forage plants. National Wool Grower 13(6):15-17.

Schmitt, J. A. 1955a. The status of the name Erysiphe cichoracearum DC. Mycholgia 47:422-424.

________. 1955b. The host specialization of Erysiphe cichoracearum DC. Mycholgia 47:688-701.

Skidmore, L. W., and N. F. Peterson. 1932. Observations on the toxicity of golden glow (Rudbeckia laciniata) to swine and other animals. Journal of the American Veterinarian Medical Association 81:655-662.

Smith, D. 1969. Removing and analyzing total non-structural carbohydrates from plant tissue. Research Report No. 41. Research Division, College of Agriculture and Life Science, University of Wisconsin, Madison, Wisconsin.

Southard, A. 1958. Some characteristics of five soil profiles under quaking aspen in Cache National Forest. Unpublished MS thesis, Utah State University Library, Logan, Utah.

Stevens, O. A., and L. F. Rock. 1952. Outline for ecological life history studies of herbaceous plants. Ecology 33:415-422.

Steward, F. C. 1968. Growth and organization in plants. Addison-Wesley Publishing Company, Reading, Massachusetts.

Taylor, M. E. 1963. The lower Devonian water canyon formation of Northeastern Utah. Unpublished MS thesis, Utah State University Library, Logan, Utah.

Tidestrom, I. 1925. Flora of Utah and Nevada. Vol. 25. Contributions from the United States National Herbarium, Washington, D. C.

Tisdale, S., and N. Werner. 1966. Soil fertility and fertilizer. The Macmillan Company, New York.

United States Department of Agriculture. 1960. Index of plant diseases in the United States. Agriculture Handbook No. 165. United States Department of Agriculture, Washington, D. C.

United States Department of Commerce. 1940 to 1968. Storage-gage precipitation data for Western USA. Asheville, North Carolina.

United States Geological Survey. 1965. Map of Utah: Annual and summer precipitation.

West, N. 1968. Outline for autecological studies of range grasses. Journal of Range Management 21(2):102-105.

Williams, E. J. 1964. Geomorphic features and history of the lower parts of Logan Canyon, Utah. Unpublished MS thesis, Utah State University Library, Logan, Utah.

Williams, J. S. 1948. Geology of the Paleozoic rocks in the Logan Quadrangle, Utah, and vicinity. Geological Society of America, Bulletin 59:1121-1164.

__________. 1956. Geomorphic atlas of Utah, Cache County. Utah Geological and Mineralogical Survey, Salt Lake City, Utah. Survey Bulletin 64:1-103.

Wood, B. W. 1966. An ecological life history of budsage in Western Utah. Unpublished MS thesis, Brigham Young University Library, Provo, Utah.

Worsdell, W. C. 1919. Compositae. Annals of Botany 33:421-458.

Young, J. L. 1939. Glaciation in the Logan Quadrangle, Utah. Unpublished MS thesis, Utah State University Library, Logan, Utah.

APPENDIXES

Appendix I

Periodic Precipitation Data of Tony Grove Station in 1964, 1965, 1966, and 1967 (in inches)

1964		1965	
January 1 to February 2	: 4.38	December 13, 1964 to January 10, 1965	: 8.80
February 2 to March 7	: 1.80	January 10 to January 17	: 1.00
March 7 to March 29	: 2.60	January 17 to January 31	: 6.55
March 29 to May 17	: 3.90	January 31 to March 7	: 2.10
May 17 to June 27	: 4.40	March 7 to April 4	: 1.75
June 27 to July 25	: 0	April 4 to April 23	: 2.65
July 25 to August 30	: 0.30	April 23 to May 24	: Not available
August 30 to September 27	: 0.10	May 24 to July 4	: 2.50
September 27 to November 1	: 0.15	July 4 to July 26	: 0.80
November 1 to December 13	: 6.90	July 26 to September 12	: 4.40
December 13 to January 10, 1965	: 8.80	September 12 to September 26	: 1.30
		September 26 to November 28	: 5.15
		November 28 to January 1, 1965	: 2.90
Yearly total	32.23	Yearly total	32.53

1966		
January 1 to February 6	:	0.95
February 6 to February 27	:	1.55
February 27 to April 24	:	2.70
April 24 to June 5	:	1.95
June 5 to July 17	:	1.00
July 17 to August 28	:	1.45
August 28 to September 25	:	1.25
September 25 to December 26	:	5.75
Yearly total:		16.60

1967		
December 26, 1966 to January 29, 1967	:	3.90
January 29 to March 12	:	4.85
March 12 to July 9		
July 9 to July 25	:	.20

Appendix II

Yearly Precipitation Data of Tony Grove Station

(in inches)

A. Annual

Year	Amount
1960	25.92
1961	23.45
1962	23.92
1963	24.82
1964	32.23
1965	32.53
1966	16.60

B. Average for 25 years: (1941-1966)

a. Annual	25.24
b. Three months	
(Mid-June to Mid-Sept.)	5.34

Appendix III

Relation of the Specimens of _Rudbeckia occidentalis_

Found in Utah

No.	Location	Trees	Soil	Elevation Ft.
USU 103085	Franklin County - Idaho	Aspen-conifers	colluvium	8000
USU 23096	Sawtooth, Camas, Idaho	Open-Sage, Carex	gravel loam	6300
USU 46322	Camp Tendoy, Pocatello, Idaho			
USU 32616	Shoshone Ranger St. Twin Falls			
USU 82057	S. of Clarkia			3000
USU 110207	Franklin County - Idaho		Loam	8500
USU 108409	Rainbow garden - Ogden, Ut.		Moist soil	
USU 32700	White Pine Lake	Sage park, spruce		3500
USU 102043	Sevier County-Willow Creek	Aspen		9000
USU 103070	Cache Co, Arbs Basin			
USU 3235	Ephraim Canyon	Aspen		9000
USU 20715	Maple Canyon, Ephraim			
USU 13774	Wasatch Mts, Alta			10000
USU 13776	Providence ditch, Cache			
USU 13781	Fork Canyon			5500

No.		Location	Trees	Soil	Elevation Ft.
USU	47992	Angel Lake, Rubi Mts. Elko, Nev.		Loam soil	
USU	43027	Lamance Cr. Humboldt		Sand moist	5000
USU	34568	Josephine Co.			2500
UU	64869	Crater of Moon, Ida. Butte			5000
UU	61128	Lower Kimberly-Tushar Mtns Sevier Co.	Aspen, fir		8500
UU	47779	Marysuale Canyon, Sevier Co. Deer Creek			6500
UU	16446	Reed Benson Ridge, Salt Lake Co. Cottonwood			9200
UU	2435	Salt Lake Co. Lambs Canyon			7500
UU	398	Stairs Fork. Salt Lake Big Cottonwood			6800
UU	1161	North Edge Silver Lake Brighton, Big Cottonwood Salt Lake	Aspen, fir	Granitic soil	8740
UU	21380	So. Fork George, Creek Canyon Box Elder Co.			6700
UU	19367	Brighton, Salt Lake	grassy flat		8200
UU	20811	Muller's Park, Wasatch Mo. Davis Co.			5800
UU	67712	Pioneer Range St. Millard Co.	Aspen, fir		9200
UU	21745	Ephraim Canyon, Sanpete Co.			9000
UU	19368	Mt. Timpanogas Utah Co.	Aspen belt		7500
UU	45733	Big Cottonwood Salt Lake Co.			7500
UU	9371	American Fork Canyon Utah Co.			7500

No.		Location	Trees	Soil	Elevation Ft.
UU	19372	North Fork, Provo River Utah Co.			8000
UU	45732	Mt. Timpanogos Wasatch Mt. Utah Co.			7000
UU	45729	North Fork Canyon, Weber Co.	Dry gravel soil		6500
UU	45731	East Canyon, Gogorzasu, Utah Co.			7000

VITA

Juan Arturo Florez

Candidate for the Degree of

Doctor of Philosophy

Dissertation: Ecological Life History of Rudbeckia occidentalis Nutt.

Major Field: Range Science

Biographical Information:

Personal Data: Born at Puno, Peru, June 16, 1936, son of Fidel Al. and Concepcion Florez; married Virginia Monge June 17, 1961; two children--Monica and Jessica.

Education: Attended elementary school in Puno, Peru; graduated from Colegio San Carlos High School in 1952; received the degree of Ingeniero Agronomo from Universidad Agraria-LaMolina, Lima, Peru, with a major in Agronomy, in 1958; did graduate work and completed requirements for the Master of Science degree, specializing in Agronomy at Washington State University in 1966; completed requirements for the Philosophy of Doctor degree, specializing in Range Science at Utah State University in 1971.

Professional Experience: 1959-1961, in charge Forages Program--South of Peru, Agriculture Ministry, Peru; 1962 to present, Associate Professor in Forages at the Agrarian University-LaMolina, Lima, Peru.